

Cowpea genetics: a review of the recent literature

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Abstract

In the decade since the literature on the genetics of cowpea was last reviewed by Fery (1985), researchers have published numerous cowpea genetics studies, especially on economically important traits. Both qualitative and quantitative procedures have been utilized to study these traits, and considerable effort made to increase our knowledge of cowpea cytogenetics, heterosis, and problems associated with crossing cowpea with other *Vigna* species. Many inheritance studies have addressed flower traits and earliness parameters, durations of specific developmental stages, pigmentation, nitrogen fixation, mycorrhizal colonization, seedling vigor traits, plant habit and root traits, leaf traits, pod traits, seed traits and grain quality, yield and yield components, fodder quality, heat and drought tolerances, resistance to bacterial, fungal and viral diseases, resistance to root-knot nematodes, resistance to insects, and resistance to parasitic weeds such as *Striga gesnerioides* and *Alectra vogelii*.

Introduction

The literature on cowpea (*Vigna unguiculata* [L.] Walp.) genetics was last reviewed by Fery (1985). That review covered all of the pertinent literature on cytologic, qualitative, and quantitative genetics, and included an updated list of genes and a set of rules for the gene nomenclature of *Vigna*. Our objective is to review the research on cowpea genetics in more recent literature and thus complement the earlier review.

Cytogenetics and interspecific hybridization

Three recent publications (Barone and Saccardo 1990; Pignone et al. 1990; Saccardo et al. 1992) contain detailed descriptions of the cowpea karyotype. Barone and Saccardo (1990) used pachytene bivalents to develop their karyotype. Pignone et al. (1990) developed a banded karyotype by using cells in mitotic prometaphase. Saccardo et al. (1992) used both conventional techniques and an automatic image analysis system in their work with pachytene and mitotic prometaphase and metaphase chromosomes.

Ghosh (1978) observed induced cowpea tetraploids, and noted that chromosome doubling affects many plant traits, e.g., percentage germination of seeds, nature of germination, seedling and plant survival, rate of growth, leaflet shape and color, stomata size, time and duration of flowering, flower size, pollen grain viability, number of shriveled seed per pod, and seed size.

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Fatokun and Singh (1987) successfully crossed cultivated cowpea with a hairy wild relative (*Vigna pubescence*). They used tissue culture techniques to rescue the hybrid embryos, which would otherwise have been shriveled and degenerated. The F₁ plants were vigorous in growth but were partially sterile, with only about 32% viable pollen. Cytological investigations of F₁ plants showed some meiotic abnormalities in the pollen mother cells. These abnormalities included a few univalents and quadrivalents, suggesting some structural differentiation in the chromosomes.

Barone and Ng (1990) could not obtain an interspecific cross between *V. unguiculata* and *V. vexillata*. They concluded that the following were barriers to crossability: lack of fertilization and collapse of fertilized ovules 5–8 days after pollination. All attempts by Fatokun (1991) to cross *V. vexillata* with various cultivated and noncultivated cowpeas were also unsuccessful.

Considerable progress has been made in recent years in developing innovative biotechnologies for cowpea. The focus of much of this research is on increasing our understanding of the cowpea genome and the development of techniques to insert exotic genes into the cultivated cowpea (see later in this volume: Monti et al. 1997; Fatokun et al. 1997a,b; Kononowicz et al. 1997).

Heterosis

Several studies show that cowpea hybrids can exhibit considerable heterosis for many traits. Heterosis was demonstrated for time of flowering (Adu-Dapaah et al. 1988; Lodhi et al. 1990), time to maturity (Adu-Dapaah et al. 1988), vine length (Lodhi et al. 1990), stem girth (Lodhi et al. 1990), number of pods per plant (Teofilo et al. 1984; Patil and Shete 1987; Adu-Dapaah et al. 1988), number of clusters per plant (Patil and Shete 1987), pod length (Patil and Shete 1987), number of branches per plant (Adu-Dapaah et al. 1988; Lodhi et al. 1990), leaf length (Lodhi et al. 1990), leaf breadth (Lodhi et al. 1990), plant height (Adu-Dapaah et al. 1988), number of seeds per pod (Patil and Shete 1987; Adu-Dapaah et al. 1988), grain yield per plant (Teofilo et al. 1984; Patil and Shete 1987; Adu-Dapaah et al. 1988), seed weight (Patil and Shete 1987; Adu-Dapaah et al. 1988), seed length (Patil and Shete 1987), green fodder yield (Lodhi et al. 1990), dry-matter yield (Lodhi et al. 1990), protein content of seed (Emebiri 1991), protein content of forage (Jain et al. 1980; Lodhi et al. 1990), and in vitro dry-matter digestibility of forage (Jain et al. 1980; Lodhi et al. 1990). Sherif et al. (1991) reported that F₁ hybrids displayed significantly greater resistance to drought than resistant parental cultivars.

Flower traits and earliness

Emebiri (1989b) reported that both flower size and style length are heritable, with narrow-sense heritability (H_n) estimates, calculated using variance components, of 72% and 47%, respectively. The H_n estimates for flower size and style length, calculated by regressing the mean values of F₁ plants on their mid-parent values, were 77% and 69%, respectively. Apte et al. (1987) estimated a broad-sense heritability (H_b) of 16% for number of inflorescences per plant. Brantley and Kuhn (1983) noted that plants homozygous for the *pbs* gene conditioning proliferated leaf buds were sterile (Table 1). They concluded that the sterility was caused by failure of the style to elongate. In most instances, the stigma is enclosed by united stamens.

Table 1. Cowpea gene index.

Preferred symbol	Synonym	Character†	Reference
<i>Bgs</i> [§]	<i>Bg</i>	Big seed	Karkannavar et al. (1991)
<i>cd</i> [§]		Chlorophyll deficiency	Kirchhoff et al. (1989)
<i>cpi</i>		Ineffective nodulation	Pemberton et al. (1990)
<i>gc</i>		Green cotyledon	Fery and Dukes (1994)
<i>Hbs</i>		Heat-induced browning in seed coat	Patel and Hall (1988)
<i>ims</i>		Res. to cowpea severe mosaic virus	Jimenez et al. (1989)
<i>pbs</i>		Proliferated buds	Brantley and Kuhn (1983)
<i>Pm-1</i>	<i>Pm₁</i>	Miniature plant	Singh (1980)
<i>Pm-2</i>	<i>Pm₂</i>	Miniature plant	Singh (1980)
<i>pt</i>		Nonpetiolate leaf	Fawole (1988)
<i>pt-2</i>		Nonpetiolate leaf-2	Fawole (1990)
<i>Rac</i>	<i>AC₁</i>	Res. to <i>Aphis craccivora</i>	Bata et al. (1987); Ombakho et al. (1987); Pathak (1988)
<i>Rac-2</i>	<i>AC₂</i>	Res. to <i>Aphis craccivora-2</i>	Ombakho et al. (1987); Pathak (1988)
<i>Rav-1</i>		Res. to <i>Alectra vogelii</i>	Singh et al. (1993)
<i>Rav-2</i>		Res. to <i>Alectra vogelii</i>	Singh et al. (1993)
<i>Rav-3</i>		Res. to <i>Alectra vogelii</i>	Atokple et al. (1995)
<i>rcc</i>		Res. to <i>Colletotrichum capsici</i>	Abadassi et al. (1987)
<i>rcm-1</i>		Res. to <i>Callosobruchus maculatus-1</i>	Adjadi et al. (1985)
<i>rcm-2</i>		Res. to <i>Callosobruchus maculatus-2</i>	Adjadi et al. (1985)
<i>Rsg-1</i>		Res. to <i>Striga gesnerioides</i>	Singh and Emechebe (1990)
<i>Rsg-2</i>		Res. to <i>Striga gesnerioides</i>	Atokple et al. (1995)
<i>Rsg-3</i>		Res. to <i>Striga gesnerioides</i>	Atokple et al. (1995)
<i>rss</i>		Res. to <i>Sphaceloma</i> sp.	Abadassi et al. (1987)
<i>Rsv-1</i>		Res. to <i>Septoria vignae-1</i>	Abadassi et al. (1987)
<i>Rsv-2</i>		Res. to <i>Septoria vignae-2</i>	Abadassi et al. (1987)
<i>sbc-1</i>		Res. to southern bean mosaic virus-1	Melton et al. (1987)
<i>sbc-2</i>		Res. to southern bean mosaic virus-2	Melton et al. (1987)
<i>Spg-1</i> [§]	<i>Pp-1</i>	Stem pigmentation-1	Karkannavar et al. (1991)
<i>Spg-2</i> [§]	<i>Pp-2</i>	Stem pigmentation-2	Karkannavar et al. (1991)
<i>Sti</i>		Stipule color; red dominant over green	Karkannavar et al. (1991)
<i>Vv-1</i>		<i>Uromyces vignae</i> res.-1	Chen and Heath (1993)
<i>Vv-2</i>		<i>Uromyces vignae</i> res.-2	Chen and Heath (1993)

† Res. = resistance.

§ Proposed new symbol.

Earliness is an important agronomic trait. Typically, it is measured by such criteria as days to flowering or days to maturity. A number of quantitative studies of the genetics of earliness parameters have been published in recent years (Table 2); the Hb estimates

Table 2. Estimates of broad-sense heritability (%) for earliness (days to flowering and days to pod maturity).

Reference	Days to flowering	Days to pod maturity
Apte et al. (1987)	58.1 [†] 60.8 [§]	65.0 –
Dumbre et al. (1983)	90.0	–
Jana et al. (1982)	93.0	–
Mishra et al. (1987)	52.7	–
Pandita et al. (1982)	95.6	–
Patil and Baviskar (1987)	65.3	82.9
Radhakrishnan and Jebara (1982)	–	87.8
Roquib and Patnaik (1990a)	91.0	60.0
Senanayake and Wijerathne (1988)	67.3	–
Sharma and Singhania (1992)	95.8	–
Sharma et al. (1988)	98.0	–
Siddique and Gupta (1991)	97.8	95.5
Sreekumar et al. (1979)	69.2	–
Thiyagarajan (1989)	89.0	81.0
Vaid and Singh (1983)	56.1 [¶] 16.5 [‡]	– –

† Days to initial flowering.

§ Days to 50% flowering.

¶ Derived from F₃ populations.

‡ Derived from F₄ populations.

average 75% for days to flowering and 79% for days to pod maturity. Adu-Dapaah et al. (1988) observed a tendency for dominance of early flowering and pod maturity.

Duration of specific developmental stages

Emebiri and Obisesan (1991) observed that a plant's life cycle consists of a succession of relatively distinct phases that comprise a developmental pattern, and that seed yields of crops are often influenced by the developmental pattern. They speculated that certain phases of the developmental pattern are potentially important criteria for selecting higher yields. Emebiri and Obisesan (1991) reported H_n for the following developmental stages (first estimate calculated from genetic variance components; second estimate calculated from regression of F₂ on F₁): duration of vegetative period (days), 57% and 41%; days to pod maturity, 66% and 64%; duration of pod filling (days), 42% and 52%; growth rate of pods (mg per day), 75% and 20%; and days to leaf senescence, 57% and 57%. Emebiri and Obisesan (1991) noted that all of the phases were controlled by genes with both additive and nonadditive effects. Sreekumar et al. (1979) reported an H_b estimate of 49% for the total duration of the harvest period. Dumbre et al. (1983) reported an H_b of 40% for the duration of the maturity period.

Pigmentation

Several recently published studies address the inheritance of color in cowpea. Fery and Dukes (1994) reported that a recessive gene, *gc*, conditions the green cotyledon trait. They

noted that the *gc* gene is not allelic to nor linked with the *gt* gene that conditions the green testa trait. Patel and Hall (1988) noted that a dominant gene, *Hbs*, conditions heat-induced browning in the seed coat of the heat tolerant line TVu 4552. They did not observe any close linkages between the *Hbs* gene and genes controlling heat tolerance during floral bud development or normal brown seed coat pigmentation. Karkannavar et al. (1991) reported that a single dominant gene, *Sti*, conditions stipule color. They noted that red color is dominant over green. Karkannavar et al. (1991) also reported that two duplicate genes condition stem pigmentation. They proposed the symbols *Pp-1* and *Pp-2* for these genes, but as *Pp-1* and *Pp-2* are the symbols for purple plant pigmentation genes (Fery 1985), we propose the symbols *Spg-1* and *Spg-2*. Kirchoff et al. (1989) demonstrated that a single recessive gene governs the inheritance of a mutant chlorophyll-deficiency trait. Since Kirchoff et al. (1989) did not propose a symbol for this gene, we propose the symbol *cd*.

Nitrogen fixation and mycorrhizal colonization

Several researchers have studied traits influencing nitrogen fixation and mycorrhizal colonization. Miller et al. (1986) investigated traits influencing nitrogen fixation efficiency. They reported the following Hn estimates: nodule number, 55%; nitrogenase activity, 62%; nodule weight, 39%; and top dry weight, 17%. They also demonstrated that additive gene action was important for nodule number and nitrogenase activity, and that dominance and interallelic gene action was important for nodule weight and top dry weight. Dayap and Rasco (1988) published the following Hb estimates: nitrogenase activity, 24%; secondary root nodule weight, 38%; and secondary root nodule number, 9.5%. They noted that additive gene action was important for all three traits. Roquib and Patnaik (1990a) studied the inheritance of effective root nodules at 30 and 65 days after planting (DAP). They reported the following Hb estimates for effective root nodules: main root at 30 DAP, 6%; branch root at 30 DAP, 21%; main root at 65 DAP, 36%; and branch root at 65 DAP, 11%. Pemberton et al. (1990) reported that a single recessive gene, *cp1*, conditioned the inheritance of an ineffective nodulation trait. Mercy et al. (1990) demonstrated that endomycorrhizal colonization in cowpea is heritable, with an Hb of 46%.

Seedling vigor traits

Ogunbodede (1988) found considerable genetic variability in cowpea for several seedling vigor traits. He reported Hb estimates for the following traits: emergence percentage, 89%; emergence index, 46%; emergence rate index, 46%; growth rate (9–13 DAP), 7%; growth rate (13–17 DAP), 29%; growth rate (17–21 DAP), 52%; and growth rate (21–25 DAP), 57%. Ogunbodede (1988) noted that there have been reports of positive associations between seedling vigor and yield in several crops, and suggested that specific seedling vigor traits might be useful selection criteria for yield in cowpea.

Plant habit and root traits

Singh (1980) assigned the symbols *Pm-1* and *Pm-2* to two genes conditioning miniature plant habit. Karkannavar et al. (1991) studied the tendrillar and nontendrillar plant habits, and concluded that plant habit has a trigenic mode of inheritance. Uguru and Uzo (1991) studied decumbent, climbing, and bushy plant habits, and concluded that two allelic pairs

Table 3. Estimates of broad-sense heritability (%) for growth-habit traits.

Reference	Plant height	Branches/ plant	Nodes on		Leaves/ plant	Leaf area	Root length
			main stem	Stem diameter			
Apte et al. (1987)	27.4	34.9	—	—	—	—	—
Araujo and Nunes (1983)	—	22.9	8.3	0.0	14.0	90.0	—
Dumbre et al. (1983)	78.0	—	—	—	—	—	—
Jana et al. (1982)	—	68.8	—	—	—	—	—
Pandita et al. (1982)	15.7	—	—	—	—	—	73.7
Radhakrishnan and Jebara (1982)	97.9	96.5	—	—	—	—	—
Roquib and Patnaik (1990a)	94.0	—	5.0	—	—	—	—
	—	—	7.0 [†]	—	—	—	—
Roquib and Patnaik (1990b)	89.0 [§]	—	—	—	—	74.0 [¶]	—
	86.0 [‡]	—	—	—	—	56.0 ^{††}	—
Senanayake and Wijerathne (1988)	44.5	55.8	—	—	—	—	—
Sharma and Singhanian (1992)	90.6	—	—	—	57.1	96.1	—
Siddique and Gupta (1991)	92.3	—	—	—	—	—	—
Thaware et al. (1991)	43.4	24.2	—	—	38.3	—	—
Thiyagarajan (1989)	67.8	42.6	—	—	—	—	—
Thiyagarajan et al. (1989)	97.6	96.2	—	—	—	—	—
Vaid and Singh (1983)	—	60.1 ^{§§}	—	—	—	—	—
	—	67.0 ^{¶¶}	—	—	—	—	—

† Secondary branch.

§ Early growth stage.

¶ Terminal leaflets.

‡ Rapid leaf formation stage.

†† Lateral leaflets.

§§ Derived from F₃ populations.

¶¶ Derived from F₄ populations.

govern plant habit. The works of Karkannavar et al. (1991) and Uguru and Uzo (1991) confirm conclusions drawn by earlier researchers (Fery 1985). In recent years, many researchers have used quantitative procedures to study the inheritance of growth-habit traits such as plant height, branch number, node number, stem diameter, leaf number, leaf area, and root length, and over 30 heritability estimates have been published (Table 3). Although these studies vary, their results indicate that most growth-habit traits are at least moderately heritable. For example, the average Hb estimates for plant height and branch number were 71% and 57%, respectively.

Leaf traits

Brantley and Kuhn (1983) assigned the symbol *pbs* to a recessive gene conditioning proliferated leaf buds. They observed that plants homozygous for the *pbs* gene exhibit elongated and distorted leaflets with irregular margins and abnormal vein curvature, and male sterility caused by the failure of the style to elongate. Fawole (1988) assigned the symbol *pt* to a recessive gene that governs a nonpetiolate leaf mutant. In a subsequent paper, Fawole (1990) assigned the symbol *pt-2* to a second recessive gene conditioning the nonpetiolate phenotype, and demonstrated that the *pt* and *pt-2* genes are neither allelic nor

linked. Fawole (1990) also studied the relationship between the *pt* and *pt-2* genes and the *un* gene that conditions the unifoliolate leaf trait. He found that the absence of the petiole in the unifoliolate mutant is not a pleiotropy effect of the *un* gene, as suggested by Rawal et al. (1976), but is due to a mutation of one of the genes conditioning petiole development. Fawole (1990) observed that the *un* gene exhibited both incomplete penetrance and variable expressivity, and he concluded that the gene is closely linked to one of those controlling petiole development.

Pod traits

Several recently published studies demonstrate that pod length is moderately to highly heritable; and the Hb estimates average 70% (Table 4). Additive gene effects were more important than dominance effects (Ogunbodede and Fatunla 1985). The number of seeds per pod is moderately to highly heritable; the Hb estimates average 64%. Drabo et al. (1985) observed that additive, dominance, and epistatic gene effects were of equal importance in conditioning the trait. Roquib and Patnaik (1990a) reported an Hb of 62%

Table 4. Estimates of broad-sense heritability (%) for cowpea pod and seed traits.

Reference	Pod length	Pod breadth	Seeds/pod	100-seed weight	Seed protein content
Apte et al. (1987)	62.4	–	65.8	82.5	–
Araujo and Nunes (1983)	98.0	–	68.1	95.0	–
Drabo et al. (1984)	–	–	–	85.1	–
	–	–	–	75.4 [†]	–
Drabo et al. (1985)	–	–	52.2 [§]	76.0 [§]	–
Dumbre et al. (1983)	–	–	81.0	–	–
Emebiri (1991)	–	–	–	–	70.0
	–	–	–	–	78.0 [¶]
Gowda et al. (1991)	–	–	70.2	86.0	–
Jana et al. (1982)	85.5	–	78.6	97.9	–
Nielsen et al. (1993)	–	–	–	–	95.0
Pandita et al. (1982)	32.2	–	–	–	–
Patil and Baviskar (1987)	70.3	–	33.3	90.9	–
Radhakrishnan and Jebara (1982)	91.0	–	94.5	99.6	–
Roquib and Patnaik (1990a)	76.0	62.0	–	22.0	–
Senanayake and Wijerathne (1988)	82.1	–	45.1	96.2	92.1
Siddique and Gupta (1991)	84.1	–	75.3	94.4	–
Sreekumar et al. (1979)	–	–	40.6	96.5	–
Thiyagarajan (1989)	70.8	–	71.2	83.4	–
Thiyagarajan et al. (1989)	98.6	–	99.6	–	–
Vaid and Singh (1983)	23.8 [†]	–	44.5 [†]	15.1	–
	34.0 ^{††}	–	37.5 ^{††}	–	–

† Narrow-sense heritability estimate.

§ Average of 12 estimates.

¶ Derived from a different cross.

‡ Derived from F₃ populations.

†† Derived from F₄ populations.

for pod breadth. Ogunbodebe and Fatunla (1985) demonstrated that additive gene effects are usually more important than dominance gene effects in controlling seed crowding within the pod. However, they noted that dominance gene effects can be important in some crosses.

Seed traits and grain quality

Karkannavar et al. (1991) identified a dominant gene that governs big seed. They proposed the symbol *Bg* for this gene, but *Bg* is the symbol for brown grain (Fery 1985). Therefore, we propose *Bgs* for the symbol. Ogunbodebe and Fatunla (1985) proposed a digenic epistatic model for seed size. Most recently published heritability estimates of seed size, usually measured as 100-seed weight, indicate that the trait is highly heritable; Hb estimates average 79.7% (Table 4). Drabo et al. (1984) concluded that the gene action controlling seed size is predominantly additive, but they also noted that additive \times additive epistatic effects are significant, and estimated that the minimum number of effective factors conditioning seed size is eight.

Drabo et al. (1988) examined segregating populations for eye pattern. Their results generally support the findings reported by earlier researchers (Fery 1985). However, they noted that incomplete dominance of several seed coat pattern genes might make classification rather difficult in progeny segregating for the holstein, watson, small eye, and hilum ring traits.

Published Hb estimates for protein content in seed average 80% (Table 4). Emebiri (1989a) concluded that protein content is controlled by nuclear genes, but he could not demonstrate that extra-nuclear determinants were important. In a paper published subsequently, he reported that inheritance of protein content in seed involved both additive and nonadditive gene effects, and that cytoplasmic factors might influence the trait (Emebiri 1991).

Nielsen et al. (1993) studied various aspects of grain quality in cowpea, and reported genetic variability for protein, fat, ash, carbohydrate, and cooking time. The Hb estimates were 76% for cooking time, 95% for protein, 72% for fat, 83% for ash, and 79% for carbohydrate. Protein content was negatively correlated with fat (-0.22) and carbohydrate (-0.98), and positively correlated with ash content ($+0.35$). Larger seeds and seeds with smooth seed coats took relatively longer times to cook. In view of the available genetic variability, it is possible to develop cowpea varieties with higher protein content that cook relatively quickly.

Yield

The results of many recent studies indicate that the yields of both the reproductive and the vegetative portions of the cowpea plant are moderately to highly heritable under most environmental conditions (Table 5). For example, heritability estimates for cluster number, pod number, seed yield, and fresh fodder yield average 71%, 62%, 62%, and 55%, respectively. Jatasra (1979, 1980) reported that most of the genes governing seed and green fodder yields act additively. However, he observed that nonadditive gene action was more important in conditioning dry fodder yield (Jatasra 1979). Siddique and Gupta (1991) demonstrated that additive gene effects were important in conditioning both seed yield and number of pods per plant.

Table 5. Estimates of broad-sense heritability (%) for various yield parameters.

Reference	Clusters/ plant	Pods/ cluster	Pods/ plant	Green pod wt/plant	Seeds/ plant	Seed wt/ plant	Harvest index	Fresh fodder yield	Dry fodder yield
Apte et al. 1987	-	-	14.0	-	-	17.0	20.5	-	-
Araujo and Nunes 1983	-	-	67.0	-	-	52.0	-	-	-
Dumbre et al. 1983	-	-	64.0	-	-	57.0	-	-	-
Gowda et al. 1991	-	-	80.3	-	-	85.9	-	-	-
Imrie 1986	-	-	-	-	-	63.0 [†]	67.0 [†]	-	-
	-	-	-	-	-	25.0 [§]	54.0 [§]	-	-
Jana et al. 1982	-	-	96.8	94.5	-	-	-	-	-
Mishra et al. 1987	-	-	-	-	-	27.9 [¶]	-	-	-
Pandita et al. 1982	-	-	-	-	-	91.7	-	-	-
Patil and Baviskar 1987	63.1	69.2	68.7	-	-	51.6	-	-	-
Radhakrishnan and Jebara 1982	94.1	-	98.9	-	-	99.8	-	-	-
Roquib and Patnaik 1990a	-	-	-	-	83.0	74.0	-	-	-
Roquib and Patnaik 1990b	-	-	-	-	-	-	-	14.0	24.0
Senanayake and Wijerathne 1988	-	-	31.6	-	-	90.1	-	-	-
Sharma and Singhanian 1992	-	-	-	-	-	-	-	84.4	62.0
Sharma et al. 1988	-	-	-	46.9	-	-	-	-	-
Siddique and Gupta 1991	79.3	-	92.8	-	-	94.7	-	-	-
Sreekumar et al. 1979	-	-	-	-	-	43.4	-	-	74.0 [‡]
Thaware et al. 1991	-	-	-	-	-	-	-	66.6	-
Thiyagarajan 1989	33.0	-	25.9	-	-	30.2	-	-	-
Thiyagarajan et al. 1989	98.0	-	98.6	-	-	99.8	-	-	-
Vaid and Singh 1983	51.0 ^{††}	-	38.7 ^{††}	-	-	54.5 ^{††}	-	-	-
	78.7 ^{§§}	-	27.4 ^{§§}	-	-	57.8 ^{§§}	-	-	-

† Single-row plots used to estimate yield.

§ Hill plots used to estimate yield.

¶ Narrow-sense heritability estimate.

‡ Haulms.

†† Derived from F_3 populations.

§§ Derived from F_4 populations.

Fodder quality

Several researchers have investigated the genetic nature of traits important to fodder quality. Sharma and Singhanian (1992) reported Hb estimates for dry-matter content and crude protein content of 82% and 86%, respectively. Jain et al. (1980) demonstrated a preponderance of nonadditive gene action for total protein and in vitro dry-matter digestibility. Sharma and Singhanian (1992) reported a Hb estimate for stem-leaf ratio of 96%, but Roquib and Patnaik's (1990b) estimate for the same trait was only 9%. Thaware

et al. (1991) demonstrated that Hb estimates for the components of green fodder yield, i.e., leaf yield (55%) and stem yield (62%), are smaller than the Hb estimate for green fodder yield itself (67%). Their Hb estimate for the leaf yield index [(leaf weight/weight total green forage) × 100] was only 15%.

Tolerance to heat and drought

Marfo and Hall (1992) used qualitative procedures to study the inheritance of heat tolerance during pod set, and their results suggest that heat tolerance is conditioned by a single dominant gene. However, they noted substantial environmental influence on the expression of the trait, but results of additional inheritance studies using quantitative procedures indicated that heritability is low. The Hn estimates were 24–27%, while realized heritabilities were 24–29%.

Hall et al. (1990) noted that measurements of the carbon isotope composition of plant parts can be used to estimate water-use efficiency (total biomass/transpiration) of plants, and they conducted heritability studies of carbon isotope discrimination by cowpea plants. They observed that genotypic differences were readily detected in leaves, and calculated an Hb of 76%. Ismail and Hall (1993) demonstrated that water-use efficiency and carbon isotope discrimination were strongly and negatively correlated. Using data from reciprocal crosses, they showed that both water-use efficiency and carbon isotope discrimination are controlled by nuclear genes. Both high water-use efficiency and low carbon isotope discrimination exhibited partial dominance in pot experiments. However, Ismail and Hall (1993) noted that high carbon isotope discrimination exhibited partial dominance in plants grown under natural soil conditions in a field environment.

Resistance to bacterial and fungal diseases

Development of cultivars with resistances to diseases incited by bacterial and fungal pathogens has been a major goal of most cowpea breeding programs since the early part of this century. In the past 10 years, studies on the inheritance of resistance have been published on the following diseases: bacterial blight, brown blotch, Fusarium wilt, Phytophthora, rust, scab, and Septoria leaf spot.

Prakash and Shivashankar (1984) reported that resistance to bacterial blight [*Xanthomonas campestris* pv. *vignicola* (Burk.)] is recessive, and probably inherited quantitatively, with an Hb estimate that ranged from 30 to 80% and averaged 55%. They also estimated that the minimum number of effective factors conditioning resistance was small, probably between two and four.

Abadassi et al. (1987) reported that a single recessive gene, *rcc*, governs resistance to brown blotch (*Colletotrichum capsici* [Syd] Butler and Bisby). They observed partial dominance of susceptibility over resistance. They also reported that a recessive gene, *rss*, governs resistance to scab (*Sphaceloma* sp.), and duplicate dominant genes, symbolized by *Rsv-1* and *Rsv-2*, govern resistance to Septoria leaf spot (*Septoria vignae* P. Henn).

Rigert and Foster (1987) studied the inheritance of resistances to Fusarium wilt incited by race 2 and race 3 of *Fusarium oxysporum* f. sp. *tracheiphilum* (E. F. Sm.) Synder and Hansen. They found that the cultivar California Blackeye 3 possesses both a single dominant gene that conditions resistance to race 3 and a single incompletely dominant gene that conditions resistance to race 2. Conversely, they found that the breeding line 7964

possesses both a single dominant gene that conditions resistance to race 2 and a single incompletely dominant gene that conditions resistance to race 3. Rigert and Foster (1987) decided not to propose symbols for the resistance genes in California Blackeye 3 and 7964 because the nature of the relationship between the genes was not clear. Fang and Hwang (1987) studied resistance to Fusarium wilt in yardlong bean, and concluded that the resistance is likely governed by a single recessive gene.

Bateman et al. (1989) investigated the nature of inheritance of resistance to stem and root rot incited by race 2 of *Phytophthora vigna* Purss. They demonstrated that resistance was conditioned by a single dominant gene. The relationship between this gene and the *Sr* gene that conditions resistance to stem rot is unclear (Fery 1985).

Chen and Heath (1993) reported that two genes, *Uv-1* and *Uv-2*, are responsible for the rust (*Uromyces vignae* Barclay) resistance exhibited by the cultivar Dixie Cream. Resistance is only partially dominant, but is effective against both the monokaryon and dikaryon forms of the fungus.

Resistance to viral diseases

Plant resistance is often the only feasible method of controlling virus diseases in cowpea. Since the review by Fery (1985), studies on the inheritance of resistance have been published for the following viruses (see also, later in this volume, Hampton et al. 1997): blackeye cowpea mosaic virus, cowpea aphid-borne mosaic virus, cowpea mosaic virus, cowpea severe mosaic virus, tobacco ringspot virus, and southern bean mosaic virus.

Two reports (Melton et al. 1987; Ouattara and Chambliss 1991) concluded that resistance to blackeye cowpea mosaic virus is conditioned by a single dominant gene. These results confirm earlier published work (Fery 1985).

Patel et al. (1982) reported on preliminary studies of the inheritance of both immunity and resistance to a strain of cowpea aphid-borne mosaic virus from Tanzania. They concluded that immunity was likely conditioned by a single recessive gene and several modifier genes. The resistance was shown to be partially dominant over susceptibility.

Data published in three reports (Eastwell et al. 1983; Bruening et al. 1987; Ponz et al. 1988) suggest that resistance to cowpea mosaic virus is conditioned by a single dominant gene.

Jimenez et al. (1989) reported that a single recessive gene, *ims*, conditions resistance to cowpea severe mosaic virus. Umaharan (1990) found that resistance to a Trinidad isolate of the virus is expressed as immunity, tolerance, and resistance. He concluded that the trait was conditioned by three major genes acting in a dosage-dependent manner.

Two reports (Bruening et al. 1987; Ponz et al. 1988) concluded that resistance to tobacco ringspot virus is governed by a single dominant gene. These findings confirm results published earlier by others (Fery 1985).

Melton et al. (1987) reported the resistance to southern bean mosaic virus-cowpea strain is conditioned by two recessive genes, *sbc-1* and *sbc-2*. Hobbs et al. (1987) studied three sources of resistance to this virus. Their data suggest that a partially dominant gene conditions the moderate nonnecrotic resistance exhibited by the cultivar Early Pinkeye, three or more genes with incomplete dominance condition the nonnecrotic resistance exhibited by the cultivar Iron, and a partially dominant gene with modifiers conditions the extreme nonnecrotic resistance exhibited by PI 186465.

Resistance to root-knot nematodes

Singh and Reddy (1986) reported that resistance to the southern root-knot nematode (*Meloidogyne incognita* [Kofoid & White] Chitwood) is conditioned by a single dominant gene, confirming the results that had been published earlier by others (Fery 1985). Fery et al. (1994) characterized several new sources of resistance to root-knot nematodes. They suggested that the allele at the *Rk* locus in these lines may not be the *Rk* allele for root-knot nematode resistance, but another allele that conditions an enhanced, dominant type resistance.

Resistance to insects

Resistance to insects is potentially a valuable means of control, either as a sole control measure or as an adjunct to other control measures. Recent publications report studies on the inheritance of resistance to the following insect pests: aphids, cowpea seed beetles (bruchids), and lygus bugs.

Three publications (Bata et al. 1987; Ombakho et al. 1987; Pathak 1988) report the results of inheritance studies of aphid (*Aphis craccivora* Koch) resistance in germplasm developed at the International Institute of Tropical Agriculture. Each publication reported that resistance is conditioned by a single dominant gene. Bata et al. (1987) and Pathak (1988) proposed that this gene be designated *Rac*, but Ombakho et al. (1987) proposed the symbol *Ac₁*. Since the Bata et al. (1987) manuscript was the earliest to be submitted for publication, we propose that the *Rac* symbol be used. Ombakho et al. (1987) and Pathak (1988) also reported the identification of a second dominant gene for aphid resistance that was the result of an induced mutation in a susceptible cultivar. Ombakho et al. (1987) proposed that the second gene be symbolized *Ac₂*, but Pathak (1988) proposed the symbol *Rac-2*. Since the Pathak (1988) manuscript was actually the earliest submitted for publication, we proposed that the *Rac-2* symbol be used. Both Ombakho et al. (1987) and Pathak (1988) concluded that the *Rac* and *Rac-2* genes are neither allelic nor linked.

Redden (1983) studied the inheritance of the seed resistance factor to cowpea seed beetles or bruchids (*Callosobruchus maculatus* [F.]) and concluded that the trait is inherited in a recessive manner. He found evidence for both digenic control and monogenic control with one or more modifier genes. Redden et al. (1983) reported that the seed resistance factor is mainly determined by the maternal genotype, that cytoplasmic effects are not important, that resistance is conditioned by major genes with presence of modifiers, and that trypsin inhibitors are associated with the resistance. Adjadi et al. (1985) found that the seed resistance factor is controlled by two recessive genes. They proposed the symbols *rcm-1* and *rcm-2* for the genes, and confirmed that the genotype of the maternal plant, not the genotype of the seed, controls resistance. Fatunla and Badaru (1983) studied the inheritance of the pod resistance factor to bruchids. They concluded that there is a cytoplasmic aspect to pod resistance, and that the chromosomal factors had both additive and dominance components. Rusoke and Fatunla (1987) investigated the mode of inheritance of both the seed resistance and pod resistance factors. They concluded that the seed resistance factor is controlled by cytoplasmic factors and two unlinked recessive genes, that the pod resistance factor is controlled by cytoplasmic factors and a partially dominant gene, and that the nuclear genes conditioning the two types of resistances are independently inherited.

Bosque-Perez et al. (1987) conducted inheritance studies on two types of resistance to the western plant bug (*Lygus hesperus* Knight), i.e., inhibition of nymphal growth (antibiosis) and resistance to seed damage. The Hb estimates for the antibiosis factor ranged from 4% to 43%, and averaged 29%, and those for resistance to seed damage ranged from 49% to 75%, and averaged 63%.

Resistance to parasitic weeds

Singh and Emechebe (1990) reported that a single dominant gene, designated *Rsg*, conditions resistance to *Striga* (*Striga gesnerioides* [Willd.] Vatke). Singh et al. (1993) found that duplicate dominant genes, designated *Rav-1* and *Rav-2*, control resistance to *Alectra* (*Alectra vogelii* Benth). Atokple et al. (1993) demonstrated that the genes conditioning the resistances to *Striga* and *Alectra* are neither allelic nor linked. Atokple et al. (1995) reported the results of extensive allelism tests among cowpea lines resistant to *Striga* and *Alectra*. This work revealed that different genes are responsible for the *Striga* resistances exhibited by B301, IT82D-849, and Suvita-2. Atokple et al. (1995) also reported that a single dominant gene conditioning *Alectra* resistance in IT81D-994 is not one of the two duplicate dominant genes conditioning resistance in B301. They proposed the symbols *Rsg-1*, *Rsg-2*, and *Rsg-3* for the genes conditioning resistance to *Striga gesnerioides* in B301, IT82D-849, and Suvita-2, respectively. They proposed the symbols *Rav-1* and *Rav-2* for the genes conditioning resistance to *Alectra vogelii* in B301, and the symbol *Rav-3* for the gene conditioning the resistance in IT81D-994.

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