

Chapter 15

Accelerated Breeding of Cowpea [*Vigna unguiculata* (L.) Walp.] for Improved Yield and Pest Resistance



**B. Rajasekhar Reddy, K. Nagendran, B. Singh, P. M. Singh, J. Singh,
and Maneesh Pandey**

15.1 Introduction

Cowpea [*Vigna unguiculata* (L.) Walp.] is a legume crop cultivated worldwide as pulse, vegetable, forage, green manure and cover crop (Smartt 1990). Due to its high protein content in leaves, pods and grains, it is widely regarded as “poor man’s meat” (Boukar et al. 2018). The primary centre of origin is Africa because it has high genetic diversity there. Cowpea can be grown easily in low fertility soils (Eloward and Hall 1987) and has the ability to fix atmospheric nitrogen like many other legumes (Ehlers and Hall 1996). Cowpea is one of the most tolerant legumes to drought because of its ability to grow in areas without irrigation and irregular rainfall (Agbicodo et al. 2009). It is one of the best crops that fit well in rice-wheat cropping systems.

The cowpea seed contains protein (23–32%), carbohydrate (17.50–60%) (Khalid and Elharadallou 2013; Kirse and Karklina 2015) and fat (1%) (Kirse and Karklina 2015) on dry weight basis. Compared to cereal and tuber crops, two- to fourfold more protein is present in cowpea (Sebetha et al. 2014; Trehan et al. 2015). Apart from this, it also contains soluble and insoluble fibre, phenolic compounds, miner-

B. R. Reddy (✉) P. M. Singh
Division of Crop Improvement, ICAR-Indian Institute of Vegetable Research, Varanasi, India

K. Nagendran
Division of Crop Protection, ICAR-Indian Institute of Vegetable Research, Varanasi, India

B. Singh
Narendra Dev University of Agriculture and Technology, Kumarganj, Ayodhya, India

J. Singh
ICAR-Indian Institute of Vegetable Research, Varanasi, India

M. Pandey
ICAR-Indian Institute of Vegetable Research, Jakhini (PO), Varanasi, India

als and B group vitamins along with many other functional compounds which are health promoting (Mudryj et al. 2012; Liyanage et al. 2014) The tender green pods of cowpea are rich in crude protein (3.2%), iron (2.5 mg per 100 g), calcium (80 mg per 100 g), phosphorus (74 mg per 100 g), vitamin A (941 IU per 100 g), vitamin C (13 mg per 100 g) and dietary fibre (2 g per 100 g), making it an excellent vegetable (Singh et al. 2001).

The worldwide production of pulse cowpea is 7.41 million tonnes cultivated in an area of 12.58 million hectares with an average productivity of 589 kg/ha. The leading cowpea-producing countries (Table 15.1) are Nigeria (340,992 tonnes) followed by Niger (1,959,082 tonnes) grown in an area of 3,782,760 ha and 5,178,517 ha, respectively. In terms of productivity (Table 15.2), leading countries are Palestine (3929.40 kg/ha) followed by Egypt (3677.20 kg/ha) (FAOSTAT 2019).

Accelerated development of varieties should be combined with speedy dissemination of developed varieties and agile withdrawal of obsolete varieties. To reduce the risk of obsolete varieties which were developed a decade ago in a different climate than today's scenario should be replaced with varieties developed within one

Table 15.1 Leading cowpea-producing countries in the world (FAOSTAT 2019)

S. no.	Country	Area (ha)	Production (tonnes)	Productivity (kg/ha)
1.	Nigeria	3,782,760	3,409,992	901.50
2.	Niger	5,178,517	1,959,082	378.30
3.	Burkina Faso	1,254,934	603,966	481.30
4.	United Republic of Tanzania	203,540	200,940	987.20
5.	Cameroon	222,625	198,201	890.30
6.	Myanmar	141,190	178,582	1264.80
7.	Kenya	260,036	146,342	562.80
8.	Mali	282,736	145,018	512.90
9.	Sudan	303,255	129,856	428.20
10.	Mozambique	331,213	87,723	264.90
11.	Democratic Republic of the Congo	170,208	72,580	426.40
12.	Senegal	159,321	59,157	371.30
13.	Malawi	100,684	48,168	478.40
14.	Haiti	40,198	28,920	719.40
15.	Peru	17,912	20,341	1135.60
16.	USA	11,655	19,822	1700.70
17.	Serbia	4733	15,968	3373.60
18.	China, mainland	18,112	15,626	862.70
19.	Madagascar	15,000	13,000	866.70
20.	Uganda	25,892	12,015	464.00
21.	Sri Lanka	6807	8576	1259.90
22.	North Macedonia	2234	7974	3568.70
23.	Mauritania	22,193	7890	355.50

Table 15.2 Top five countries leading in cowpea productivity (FAOSTAT 2019)

S. no.	Country	Area (ha)	Production (tonnes)	Productivity (kg/ha)
1.	Palestine	38	148	3929.40
2.	Egypt	1932	7104	3677.20
3.	North Macedonia	2234	7974	3568.70
4.	Serbia	4733	15,968	3373.60
5.	Trinidad and Tobago	160	505	3161.30

decade. To achieve this cowpea breeding system is to be strengthened with free international exchange of germplasm, elite varieties, speed breeding, increasing the selection intensity, large-scale phenotyping and marker- and genomics-assisted selection for accuracy (Atlin et al. 2017).

15.2 Genetic Diversity and Taxonomy

Large amounts of cowpea landraces and cultivated cowpeas were present in West and Central Africa (Padulosi and Ng 1997) which is considered as the centre of origin of cowpea. Different organizations of the world hold around 36,383 cowpea germplasm (Table 15.3) under ex situ conservation (Dumet and Fatokun 2010). Apart from this, the National Bureau of Plant Genetic Resources, New Delhi, holds 5000 germplasm of cowpea under ex situ condition as exhibited in cowpea germplasm field day held on 22 October 2019. Out of the total germplasm stored under ex situ condition, the majority (60%) of the accessions were farmers' varieties/landraces, 5.2% are breeding lines, 2.0% are wild and the remaining up to 31% that were unknown are not documented (Dumet and Fatokun 2010).

Based on the characteristics of pod, seed and ovule, the cultivated types of cowpea (Table 15.4) have been divided into five cultivar groups (Pasquet 1998, 1999). Among them *unguiculata* is the largest cultivar group. The vegetable cowpea cultivar group *sesquipedalis* (also known as yardlong bean, asparagus bean, snake bean and long bean) has more than 16 ovules and seeds spaced apart within the pod (OECD 2016).

The *Vigna unguiculata* subspecies cultivated in India were *V. unguiculata* ssp. *unguiculata* and *V. unguiculata* ssp. *biflora* grown predominantly for pulse purpose, whereas *V. unguiculata* ssp. *sesquipedalis* (yardlong bean) is grown for its immature pods as vegetable. The vegetable cowpea is grown widely in India, China, Sri Lanka, Bangladesh, Indonesia and the Philippines (Pant et al. 1982; Chakraborti 1986; OECD 2016).

The classification and nomenclature of *Vigna unguiculata* species complex was done by several workers, viz. Verdcourt (1970), Marechal et al. (1978), Mithen and Kebblewhite (1993), Padulosi (1993) and Pasquet (1993/1998). Presently the *Vigna unguiculata* species complex has been divided into 11 subspecies (Padulosi 1993; Pasquet 1993a, b, 1997; Padulosi and Ng 1997) (Table 15.5). There exists a varying

Table 15.3 Number of cowpea accessions reported from various international holders under ex situ condition

Genebank	Number of cowpea accessions	Year of introduction
Angola (SADC)	172	Non-specified
AVRDC-Taiwan	322	1984
Belgium	331	1965
Benin	155	1978
Botswana (SADC)	49	Non-specified
Cote d'Ivoire	126	1990
Germany	291	1922
IITA	15,276	1971
Kenya	875	1979
Malawi (SADC)	83	Non-specified
Mauritius (SADC)	3	Non-specified
Mozambique (SADC)	29	Non-specified
Namibia (SADC)	57	Non-specified
Nigeria	384	1987
Russia	1945	1921
South Africa	886	2005
South Africa (SADC)	55	Non-specified
South Korea	910	1987
Spain	466	1981
Swaziland (SADC)	45	Non-specified
Tanzania	386	1993
Tanzania (SADC)	39	Non-specified
Togo	100	2004
USA (USDA)	8043	1936
USA (UCR)	550	1980
Zambia (SADC)	305	Non-specified
Total	36,383	

Adopted from Dumet and Fatokun (2010) document on Global Strategy for the Conservation of Cowpea (*Vigna unguiculata* subsp. *unguiculata*)

Table 15.4 The five cultivar groups of cultivated cowpea *V. unguiculata* ssp. *unguiculata* (OECD 2016)

Cultivar group	Main features
<i>unguiculata</i>	Contains most African grain and forage types. Pods contain more than 16 ovules/pod
<i>melanophthalmus</i>	These are black-eyed pea types with less than 17 ovules per pod. Americas are the main growing areas
<i>biflora</i> (Catiang)	The pods are short and erect with smooth seed and less than 17 ovules per pod. Common in India.
<i>sesquipedalis</i>	The pods are very long and fresh tender pods are consumed. Also called as yardlong beans or asparagus bean. Especially grown in China and India
<i>textilis</i>	This cultivar group is rare and has very long peduncles. In Africa this cultivar group was once used as fibre

Table 15.5 Classification of *Vigna unguiculata* (L.) Walp. and its subspecies complex (Pasquet 1993a, b, 1997)

S. no.	Subspecies	Growth habit	Domestication	Pollination
1.	<i>unguiculata</i>	Annual	Cultivated	Self-pollinated
2.	<i>dekindtiana</i>	Perennial	Wild	Self-pollinated
3.	<i>alba</i>	Perennial	Wild	Self-pollinated
4.	<i>baoulensis</i>	Perennial	Wild	Cross-pollinated
5.	<i>letouzeyi</i>	Perennial	Wild	Cross-pollinated
6.	<i>burundiensis</i>	Perennial	Wild	Cross-pollinated
7.	<i>pawekiae</i>	Perennial	Wild	Cross-pollinated
8.	<i>aduensis</i>	Perennial	Wild	Cross-pollinated
9.	<i>tenuis</i>	Perennial	Wild	Self-pollinated
10.	<i>stenophylla</i>	Perennial	Wild	Self-pollinated
11.	<i>pubescens</i>	Perennial	Wild	Self-pollinated

degree of crossability of the ten wild subspecies with the sole cultivated cowpea subspecies. The subspecies *dekindtiana*, *alba*, *tenuis* (and var. *spontanea*), *stenophylla* and *pubescens* were previously under *dekindtiana* subspecies, so-called conveniently as *dekindtiana* group. The subspecies *baoulensis*, *letouzeyi*, *burundiensis*, *pawekiae* and *aduensis* were previously under subspecies *mensis* and conveniently called as *mensis* group. The cultivated cowpea along with *dekindtiana* group was highly self-pollinated, whereas the *mensis* group was cross-pollinated (OECD 2016).

The two botanical varieties of annual cowpea are *Vigna unguiculata unguiculata* var. *unguiculata* which is cultivated and *V.u.u* var. *spontanea* which is a wild form. The immediate progenitor of the cultivated cowpea is *V. unguiculata* ssp. *dekindtiana* sensu Verdc (*V. unguiculata* var. *spontanea* (Schweinf.) Pasquet) (Padulosi and Ng 1997).

15.3 Genetics

Cowpea is a diploid with a chromosome number of $2n = 22$. Genetics of cowpea were reviewed comprehensively by Fery (1980, 1985), Fery and Singh (1997), Singh (2002) and Boukar et al. (2018). The genetic control of various traits was presented (Table 15.6).

In vegetable cowpea breeding, both additive and dominance variances control the trait expression. High amount of variance was observed for number of pods per plant, pod yield, pod length and crude fibre content (Subbiah et al. 2013). Genetic analysis studies had shown that in vegetable cowpea, number of clusters per plant had high additive and additive \times additive genetic component, while the pod weight had high broad and narrow-sense heritability suggesting that these traits should be focused during early generation selection. Selection for pod yield should be done in

Table 15.6 Genetic control of various traits in cowpea

S. no.	Trait	Number of genes involved	References
1.	Pod pigmentation	Digenic	Mustapha and Singh (2008)
2.	Pod tip pigmentation	Monogenic and digenic	Mustapha and Singh (2008)
3.	Growth habit	Monogenic	Lachyan et al. (2016)
4.	Flower colour	Monogenic	Lachyan et al. (2016)
5.	Seed coat colour	Monogenic	Lachyan et al. (2016)
6.	Seed coat colour pattern	Monogenic	Lachyan et al. (2016)
7.	100-seed weight	Five genes	Lopes et al. (2003)
8.	Stipules	Monogenic	Pandey and Dhanasekar (2004)
9.	Cowpea aphid-borne mosaic virus (CABMV)	More than one recessive gene	Orawu et al. (2013)
		Two dominant genes	Barro et al. (2016)
10.	Bacterial blight	One or two or three recessive genes	Patel (1981)
11.	Black eye cowpea mosaic virus	Single dominant gene	Fery (1985), Melton et al. (1987) and Ouattara and Chambish (1991)
12.	Cowpea aphid-borne mosaic virus	Single recessive gene with modifier genes with partial dominance	Patel et al. (1982)
13.	Cowpea mosaic virus	Single dominant gene	Eastwell et al. (1983), Bruening et al. (1987) and Ponz et al. (1988)
14.	Cowpea severe mosaic virus	Single recessive gene	de Jimenez et al. (1989)
15.	Southern bean mosaic virus	Two recessive genes	Melton et al. (1987)
16.	Southern root-knot nematode	Single dominant gene	Singh and Reddy (1986)
17.	Aphid resistance	Single dominant gene	Bata et al. (1987), Ombakho et al. (1987) and Pathak (1988)
18.	Bruchid resistance	Seed resistance controlled by two unlinked recessive genes and cytoplasmic factors	Rusoke and Fatunla (1987)
		Pod resistance controlled by partially dominant gene and cytoplasmic factors	Rusoke and Fatunla (1987)

later generations, and for multilocation testing of yield stability number of pods per plant may be used as a criterion (Pathmanathan et al. 1997). Green pod yield per plant showed positive significant correlation with pod length, ten pod weight and number of seeds per pod. The path coefficient analysis indicated that the highest positive direct effect on green pod yield per plant was exhibited by the number of

green pods per plant followed by days to 50% flowering, ash content and pod length (Hitiksha et al. 2014).

An effective cowpea breeding strategy involves combining the erect, determinate and early maturing characters of cv. *Unguiculata* (ssp. *unguiculata*) or *Biflora* (ssp. *cylindrica*) genotypes with the long, succulent and fleshy podded characters of cv. *Sesquipedalis* (ssp. *sesquipedalis*) genotypes. Crossing between genotypes of *sesquipedalis* and those of *unguiculata* and *cylindrica* revealed low success due to specific cross combinations, genetic divergence and environment. Additive genetic variance was predominant for pod length and weight and protein content in pods and seeds. Selection in the advanced generations should be based on bushy or less viny, high-yielding segregates with appreciable protein contents in pods and seeds (Hazra et al. 2007).

15.4 Improved Varieties of Cowpea

The International Institute for Tropical Agriculture (IITA) developed several pulse-type cowpea varieties (Table 15.7) with high yield ranging from 1.5 to 2 tonnes per hectare. The improved varieties of IITA viz., IT-16 (1400 kg/ha), IT-18 (1510 kg/ha), IT-04 K-321-2 (1460 kg/ha), IT-97 K-390-2 (1370 kg/ha) and IT-99 K-494-4 (1660 kg/ha) matures in about 90-94 days and are tolerant to drought, leaf spot and bacterial diseases and have a reddish-brown seed colour. All these IITA developed varieties have protein content of more than 25% (Lopez 2019). The variety IT99K-494-6 is an Alectra-resistant variety (Boukar et al. 2012). The pulse type of cowpea gives a maximum yield of 1.5 to 2.0 tonnes per hectare, whereas by cultivating vegetable cowpea bush varieties (Table 15.8), the maximum yield of up to 15–18 tonnes per hectare can be taken in 6–8 pickings based on the variety cultivated. But for cultivating vegetable cowpea, irrigation is required at regular intervals, and the first harvest of stringless tender pods is taken 55 days after sowing.

Table 15.7 Improved varieties of cowpea by IITA

Cowpea variety	Year of release	Country	References
IT97K-499-35	2008	Nigeria	Boukar et al. (2012)
IT89KD-288, IT89KD-391	2009	Nigeria	Boukar et al. (2012)
IT97K-499-35, IT97K-499-38, IT98K-205-8	2009	Niger	Boukar et al. (2018)
IT97K-499-35, IT93K-876-30	2010	Mali	Boukar et al. (2018)
IT99K-573-1-1	2010	Niger	Boukar et al. (2018)
IT99K-573-1-1, IT99K-573-2-1	2011	Nigeria	Boukar et al. (2012)

(continued)

Table 15.7 (continued)

Cowpea variety	Year of release	Country	References
IT97K-1069-6, IT00K-1263 and IT82E-16	2011	Mozambique	Boukar et al. (2012)
IT99K-494-6	2011	Malawi	Boukar et al. (2012)
IT99K-7-21-2-2-1, IT99K-573-1-1	2012	Tanzania	Boukar et al. (2018)
IT99K-573-2-1, IT98K-205-8	2013	Burkina Faso	Boukar et al. (2018)
IT95K-193-12	2013	Benin	Boukar et al. (2018)
IT-16, IT-18, IT-04 K-321-2, IT-97 K-390-2 and IT-99 K-494-4	2015	Swaziland	Lopez (2019)
IT00K-1263, IT99K-1122	2015	Tanzania	Boukar et al. (2018)
IT07K-292-10, IT07K-318-33	2015	Nigeria	Boukar et al. (2018)
IT99K-573-2-1, IT99K-573-1-1	2015	Sierra Leone	Boukar et al. (2018)
IT99K-573-2-1, IT99K-573-1-1	2016	Ghana	Boukar et al. (2018)
IT90K-277-2, IT07K- 211-1-8	2016	South Sudan	Boukar et al. (2018)
IT99K-573-2-1 and IT98K-205-8	2019	Burkina Faso	Lopez (2019)

Table 15.8 Improved varieties of vegetable cowpea in India

S. no.	Variety	Yield (q/ha)	Developing organization	Country	Breeding method
1.	Kashi Kanchan	150–175	IIVR, Varanasi	India	Back cross pedigree selection
2.	Kashi Nidhi	125–150	IIVR, Varanasi	India	Pedigree selection
3.	Kashi Gauri	100–125	IIVR, Varanasi	India	Pedigree selection
4.	Kashi Unnati	125–150	IIVR, Varanasi	India	Pedigree selection
5.	Kashi Shyamal	80–100	IIVR, Varanasi	India	Selection from local collection Kala Jhamla
6.	Arka Garima	75–100	IIHR, Bengaluru	India	Pedigree selection
7.	Arka Samrudhi	75–100	IIHR, Bengaluru	India	Pedigree selection
8.	Arka Suman	75–100	IIHR, Bengaluru	India	Pedigree selection
9.	Pusa Komal	75–100	IARI, New Delhi	India	Pedigree selection
10	Swarna Harita	100–125	HARP, Ranchi	India	Selection



Fig. 15.1 Symptoms of cowpea golden mosaic disease on cowpea line VRCP-195-2

15.5 Breeding Cowpea for Pest Resistance

15.5.1 Cowpea Golden Mosaic Disease Resistance

In cowpea, infections caused by viruses are the most important as they can reduce the production from 60% to 80% in susceptible varieties. Among them, cowpea golden mosaic disease (CPGMD) is of prime importance causing extensive losses of 40–78% in production (Santos and Freire-Filho 1984). This disease is caused by begomovirus of the Geminiviridae family. The main symptom (Fig. 15.1) was golden mosaic of the leaves which then coalesces and cause complete yellowing of the leaves. The vector for transmission is whitefly. Resistance to CPGMD is attributed to two dominant and independent genes (Sangwan and Rish 2004) and single dominant gene (Kumar et al. 1994; Rodrigues et al. 2012). In Brazil, three AFLP markers, E.AAC/M.CCC515, E.AGG/M.CTT280 and E.AAA/M.CAG352, were found linked to CGMV resistance gene at 50.4, 24.4 and 28.7 LOD scores, respectively (Rodrigues et al. 2012). The cowpea golden mosaic DNA A virus isolates from India and Nigeria has similarity of only 62% which indicates that there exists a great viral diversity in cowpea golden mosaic virus isolates globally (Winter et al. 2002).

To identify the cowpea genes that confer durable resistance to CPGMD, we should use defined gemini virus isolates for controlled inoculation of indicator cowpea genotypes where it produces typical golden mosaic symptoms consistently in proven susceptible genotypes and no symptoms in resistance genotypes (Singh et al. 1997). Another feasible method for transmission of the virus is by grafting the diseased plant scion onto host plant root stock by top cleft or side cleft grafting. For better success, the rootstock and scion should be of similar thickness (Green 1991).

15.5.2 *Cercospora Resistance*

In humid tropics, *Cercospora* leaf spot (CLS) (Fig. 15.2) is an important disease of cowpea causing a yield loss from 36% to 42% (Schneider et al. 1976; Fery et al. 1977). *Cercospora* leaf spot-causing pathogens in cowpea are *Pseudocercospora cruenta* (Deighton 1976) and *Cercospora apii* s. lat. emend. (Crous and Braun 2003). Booker and Umaharan (2008) developed four crosses from the above four resistant genotypes and two susceptible genotypes CB27 and Los Banos Bush Sitao no.1 and developed six populations (Parent 1, Parent 2, F1, F2, BC1 and BC2) for



Fig. 15.2 *Cercospora* infestation on leaves of CP2 vegetable cowpea variety

each cross combination to know the genetics of inheritance to *Cercospora* leaf spot disease caused by *Pseudocercospora cruenta* in cowpea. He also observed that there was a differential resistance to both the pathogens among the tested cowpea varieties. For *P. cruenta* alone, four genotypes, VRB-10, IT-86D-719, IT87D-939-1 and IT-87D-792, were found resistant. Booker and Umaharan (2008) developed four crosses from the above four resistant genotypes and two susceptible genotypes CB27 and Los Banos Bush Sitao no.1 and developed six populations (Parent 1, Parent 2, F1, F2, BC1 and BC2) from each cross to know the genetics of inheritance to *Cercospora* leaf spot disease caused by *Pseudocercospora cruenta* in cowpea. These populations were screened under induced epiphytotic conditions in four separate field experiments. The onset of CLS disease varied from 35 to 48 days after sowing. The results from this study showed that resistance to CLS is governed by genetic mechanisms varying from monogenic, oligogenic to polygenic inheritance. In the cross CB27 × IT86D-719, intermediate level of resistance was found in F1 generation, and normal distribution was observed in F2 generation for CLS disease which confers polygenic resistance. Oligogenic inheritance was observed in other three crosses. In the cross CB27 × IT87D-939-1, single gene model with incomplete dominance was observed followed by single gene model with complete dominance in the cross CB27 × VRB-10. A trigger model was observed in the cross Los Banos Bush Sitao × IT86D-792 where three major genes were involved. In all these crosses, the role of minor genes was also observed. Based on symptomatic to non-symptomatic plants' ratio, these probable inheritance mechanisms were observed.

15.5.3 Anthracnose Resistance

In cowpea, anthracnose is caused by *Colletotrichum lindemuthianum* which is one of the destructive diseases. Field cowpeas (*Vigna unguiculata* ssp. *cylindrica*) show various levels of resistance to this disease, whereas vegetable-type cowpeas (*Vigna unguiculata* ssp. *sesquipedalis*) are highly susceptible to this disease. The linked markers identified for this disease are ISSR primers UBC 810 and UBC 811 which have yielded markers at 1.4 and 1.5 kb in resistant genomes, respectively, whereas RAPD primer OPA02 has yielded a marker at 850 bp in susceptible genome (Pradhan et al. 2018). In cowpea, the genetics of anthracnose resistance is not reported, while in various legumes, the gene action was reported and confusing. Polygenic resistance to anthracnose was reported in common bean (Sousa et al. 2014), and the genes offering resistance were fine mapped (Sousa et al. 2015). In lupin, single dominant gene has conferred resistance to anthracnose (Yang et al. 2012).

15.5.4 Bruchid Resistance

The main storage pest of cowpea causing considerable loss is cowpea seed beetle (*Callosobruchus maculatus* (P.)) commonly known as bruchid. Apart from seed loss, it reduces the seed quality and affects germination. The bruchid resistance is

characterized by delayed and staggered infestation along with lower bruchid emergence (Singh and Singh 1989). It was observed that after infestation of 200 g cowpea seed sample in different cowpea varieties with 2 pairs of bruchid had 25–26% seeds damaged in resistant lines, while there was 95% damaged seeds in susceptible variety after storing for 103 days (Singh et al. 1985). The bruchid resistance in cowpea is governed by two pairs of recessive genes which showed that any outcrossing reduces the resistant plants' proportion in the succeeding generation. The line Tvu 2027 was identified as moderately resistant to bruchids. Apart from this, IT84S-2246-4 is another important line which has combined resistance to bruchids, aphids and thrips along with resistance to ten diseases. For bruchid resistant breeding plants should be selected in F₂ based on plant type, maturity, seed type and resistance to diseases, and then the F₃ seed from individual plant progeny of each F₂ plant was tested for bruchid and aphid resistance. Then the selected progenies from subsequent F₄, F₅ and F₆ generations were selected for insect and disease resistance along with yield (Singh and Singh 1985). A number of *Vigna* species were also screened for resistance to *Callosobruchus maculatus* and were found that *V. luteola* and *V. adenantha* were immune and *V. oblongifolia* and *V. racemosa* were moderately resistant (Ofuya 1987). The most of these *Vigna* species do not cross with cultivated *Vigna*.

15.5.5 Pod Borer Resistance

Maruca vitrata also called as legume pod borer is an important cowpea pest that causes huge yield losses between 20% and 80% if no control measures are employed. The larva of *Maruca* is the most destructive stage that causes damage mainly during reproductive stage of the plant by feeding on the young shoots, floral parts, pods and seeds. In comparison with any other insect pests of cowpea, *Maruca* causes higher yield loss (Fatokun 2009). Through conventional breeding, varieties resistant to aphids and thrips and low levels of resistance to storage weevil were developed, less progress was observed while breeding resistance to *Maruca* in cowpea. After screening several cowpea accessions along with their wild relatives, it was found that *Vigna vexillata* accessions have resistance to *Maruca vitrata* (Fatokun 2009). Strong cross-incompatibility exists between *V. vexillata* and *V. unguiculata*, making the gene transfer impossible (Fatokun 2009). The best alternative is development of transgenic cowpea against legume pod borer by using crystal proteins (Cry) and vegetative insecticidal proteins (Vips) of the *Bacillus thuringiensis* (Bt) bacterium (Bett et al. 2017). Five Vip genes, *vip3Aa35*, *vip3Afl*, *vip3Ag*, *vip3Ca2* and *vip3Ba1*, for resistance to *Maruca* pod borer were identified, cloned and over-expressed in *Escherichia coli* to produce Vip3 protein. Among these Vip3Ba1 proteins was selected as a candidate gene for cowpea transformation because of its effective larval growth inhibition. Transgenic lines with Vip3Ba protein expression were found completely free from *Maruca* pod borer in insect feeding trials. From this, it was

proposed that combining existing *cry*-transgenic cowpea and *vip*-transgenic cowpea will provide additional resistance and the greatly delay the resistance development by *Maruca* (Bett et al. 2017).

To know the genetics of transgenic cowpea carrying *CryIAb transgene*, two lines of transgenic cowpea (TCL-709 and TCL-711) containing *transgene CryIAb* were crossed with three traditional cowpea genotypes (IT97K-499-35, IT93K-693-2 and IT86D-1010) and found monogenic segregation in F2 and BC1 with 3:1 and 1:1, respectively, by using *Bt* strips analysis and also by artificial infestation of legume pod borer. As there was stable transmission in sexual generations of *cry*-transgenic cowpea under lab and field conditions, transgenic cowpea varieties for insect resistance can be developed by combining conventional breeding with marker-assisted selection (Mohammed et al. 2015).

First genetically modified cowpea resistant to pod borer was introduced in Nigeria in 2011 (Klopez 2009; Abutu 2017) and then to Burkina Faso, Ghana and Malawi (Gomes et al. 2019). The Nigerian Biosafety Management Authority (NBMA) approved the commercial release of GM cowpea on 29 January 2019 to Nigeria farmers which facilitated the release of Pod Borer-Resistant Cowpea (PBR Cowpea)-event AAT709A (Lopez 2019).

15.6 Tissue Culture Plant Regeneration Protocols for Cowpea

In many tropical legumes, limited transformation protocols were reported due to their regeneration inability under tissue culture conditions (Somers et al. 2003). As phenolic levels are high that lead to explants' oxidation, the Leguminosae family is highly recalcitrant (Anthony et al. 1999). In spite of several numerous protocols for cowpea in vitro regeneration, there was no efficient protocol in vitro regeneration due to difficulty in reproducibility and very low regeneration frequency (Anand et al. 2000).

Raveendar et al. (2009) developed a rapid highly efficient system of organogenesis in cowpea, where the seeds were pretreated for 3 days with 13.3 μM BAP and were cultured for 2–3 weeks on MSB5 medium supplemented with 6.6 μM BAP for induction of multiple shoot buds. The multiple shoot buds were transferred onto a 0.5 μM BAP amended medium for shoot elongation. On a growth regulator-free medium, the elongated shoots were rooted and then the plantlets were transferred to soil after 12 days, with a survival success of 90-95%. Here MS medium (Murashige and Skoog 1962) with B5 (Gamborg et al. 1968) vitamins (MSB5) containing 3% (w/v) sucrose and 0.7% agar supplemented with growth regulators was used. The pH of the medium was adjusted to 5.8 by using 1 M NaOH or 1 M HCl and autoclaved at 1.06 kg cm⁻² at 121 °C for 15 minutes. The incubation conditions for the culture include 25 \pm 2 °C with irradiance of 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with 16 hours of photoperiod and 55% relative humidity.

15.7 Embryo Rescue

For *Vigna* species, the medium containing MS basal nutrients (Murashige and Skoog 1962) with sucrose (88 mM), casein hydrolysate (500 mg L⁻¹) and agar (8 g L⁻¹), but devoid of plant growth regulators (EGM), was found to be the best medium for successful germination of immature embryos in four *Vigna* species, *Vigna vexillata*, *V. lanceolata*, *V. marina*, *V. luteola*, and two mung bean subspecies, *V. radiata* ssp. *radiata* and *V. radiata* ssp. *sublobata* (Palmer et al. 2002).

15.8 Genomics-Assisted Breeding

The integration of new technologies into public plant breeding programs can make a powerful step change in agricultural productivity when aligned with principles of quantitative and Mendelian genetics (Cobb et al. 2019). Cowpea (*Vigna unguiculata* L.) has a chromosome number of $2n = 22$ and an estimated genome size of 640.6 Mbp (Lonardi et al. 2019). Initially Munoz-Amatriain et al. (2017) developed a highly fragmented draft assemblies and BAC sequence assemblies of cowpea genotype IT97K-499-35, but they lacked completeness required for genome annotation, candidate gene investigation and complete genome comparisons. So, Lonardi et al. (2019) developed an assembly of the single haplotype inbred genome of cowpea genotype IT97K-499-35 by exploiting the synergies between single-molecule real-time sequencing, optical and genetic mapping and an assembly reconciliation algorithm. Repetitive elements were present in about half of the sequences assembled in cowpea that propound that differences among genome size of *Vigna* species were mainly due to the changes in Gypsy retrotransposon quantity. Based on synteny with common bean (*Phaseolus vulgaris*), revised chromosome numbering has been adopted for cowpea chromosomes (Lonardi et al. 2019).

Molecular markers permit the indirect selection for desired alleles of genes of interest, independent of the conditions and stage of crop growth (Moose and Mumm 2008). Markers were adopted for breeding in cowpea which includes 1536-SNP GoldenGate assay (Muchero et al. 2009), which has enabled the linkage mapping and QTL analysis by Luca et al. (2011), Muchero et al. (2013) and Pottorff et al. (2014) (Amatriain et al. 2017). Timko et al. (2008) published gene space sequences in IT97K-499-35 genome approximately accounting for 160 Mb. Apart from this, in the software HarvEST: Cowpea, 29,728 unigene sequences were available (harvest.ucr.edu) (Muchero et al. 2009).

15.9 Conclusion

In cowpea, the pedigree selection should be combined with marker-assisted breeding, embryo rescue technology, genomics-assisted breeding and transgenic technology to develop multiple pest-resistant cowpeas in the present-day climate change

scenario. Apart from the above technologies used for cowpea improvement, speed breeding technology for cowpea is to be standardized so that 6–8 generations can be taken in a year making the accelerated development of cowpea varieties with improved yield and pest resistance.

References

- Abutu A (2017) Brighter Days for African Farmers-As Pod-Borer Resistant Cowpea Edge Towards Commercialisation. Available from: <https://aatfnews.aatfafrica.org/?p=669>
- Agbicodo EM, Fatokun CA, Muranaka S, Visser RGF, Der CGLV (2009) Breeding drought tolerant cowpea: constraints, accomplishments, and future prospects. *Euphytica* 167:353–370. <https://doi.org/10.1007/s10681-009-9893-8>
- Amatriain M M, Mirebrahim H, Xu P et al. (2017) Genome resources for climate-resilient cowpea, an essential crop for food security. *Plant J* 89:1042–1054
- Anand RP, Ganapathi A, Ramesh A, Vengadesan G, Selvaraj N (2000) High frequency plant regeneration *via* somatic embryogenesis in cell suspension cultures of cowpea (*Vigna unguiculata* L. Walp). *In Vitro Cell Dev Biol Plant* 36:475–480
- Anthony JM, Senaratna T, Dixon KW, Sivasithamparam K, Bunn E (1999) *In vitro* regeneration of recalcitrant Australian plants. *In Vitro Cell Dev Biol* 35:1062
- Atlin GN, Cairns JE, Das B (2017) Rapid breeding and varietal replacement are critical to adaptation of cropping systems in the developing world to climate change. *Glob Food Sec* 12:31–37
- Barro A, De La Salle TJB, Dieni Z, Kiebre Z, Poda L, Sawadogo M (2016) Inheritance and the allelic relationship of resistance to Cowpea Aphid Borne Mosaic Virus (CABMV) in two cowpea genotypes, K VX640 and K VX396-4-5-2D, in Burkina Faso. *Int J Curr Microbiol App Sci* 5(8):285–292
- Bata HD, Singh BB, Singh SR, Landeinde TAO (1987) Inheritance of resistance to aphid in cowpea. *Crop Sci* 27:892–894
- Bett B, Gollasch S, Moore A, James W, Armstrong J, Walsh T, Harding R, Higgins TJV (2017) Transgenic cowpeas (*Vigna unguiculata* L. Walp) expressing *Bacillus thuringiensis* Vip3Ba protein are protected against the *Maruca* pod borer (*Maruca vitrata*). *Plant Cell Tissue Org Cult* 131:335–345
- Booker HM, Umaharan P (2007) Identification of resistance to *Cercospora* leaf spot of cowpea. *Eur J Plant Pathol* 118:401–410
- Booker HM, Umaharan P (2008) Quantitative resistance to *Cercospora* leaf spot disease caused by *Pseudocercospora cruenta* in cowpea. *Euphytica* 162:167–177
- Boukar O, Abdoulaye T, Tam M, Agrama H, Tefera H, Fatokun C, Boahen S (2012) A success tale on improving two legume crops in Africa. <http://r4dreview.iita.org/index.php/tag/cowpea/>
- Boukar O, Belko N, Chamarthi S, Togola A, Batiemo J, Owusu E, Haruna M, Diallo S, Umar ML, Olufajo O, Fatokun C (2018) Cowpea (*Vigna unguiculata*): genetics, genomics and breeding. *Plant Breed* 138:415. <https://doi.org/10.1111/pbr.12589>
- Bruening G, Ponz F, Glascock C, Russell ML, Rowhani A, Chay C (1987) Resistance of cowpeas to cowpea mosaic virus and to tobacco ringspot virus. In: Evered D, Harnett S (eds) *Plant resistance to viruses*. Wiley, Chichester, pp 23–37
- Chakraborti AK (1986) Cowpea. In: Bose TK, Som MG, Kabir J (eds) *Vegetable crops*. Naya Prakash, Calcutta, pp 603–611
- Cobb JN, Juma RU, Biswas PS, Arbelaez JD, Rutkoski J, Atlin G, Hagen T, Quinn M, Ng EH (2019) Enhancing the rate of genetic gain in public-sector plant breeding programs: lessons from the breeder's equation. *Theor Appl Genet* 132:627–645
- Crous PW, Braun U (2003) *Mycospaerella* and its anamorphs: 1. Names published in *Cercospora* and *Passalora*. Centraalbureau voor Schimmelcultures (CBS), Utrecht

- de Jimenez CCM, Borges FOL, Debrot CEA (1989) Herencia de la resistencia del frijol (*Vigna unguiculata* [L.] Walp.) al virus del mosaico severo del caupi. *Fitopatologia Venezolana* 2(1):5–9. (English summary)
- Deighton FC (1976) Studies on *Cercospora* and allied genera. VI. *Pseudocercospora* Speg., *Pantospora* Cif. and *Cercoseptoria* Petr. *Mycol Pap* 140:1–168
- Dumet D, Fatokun C (2010) Global strategy for the conservation of cowpea (*Vigna unguiculata* subsp. *unguiculata*). Document by International Institute for Tropical Agriculture
- Eastwell KC, Kiefer MC, Bruening G (1983) Immunity of cowpeas to cowpea mosaic virus. In: Goldberg RB (ed) *Plant molecular biology. UCLA Symposia on molecular and cell biology, New series, vol XII*. Alan R. Liss, New York, pp 201–211
- Ehlers JD, Hall AE (1996) Genotypic classification of cowpea based on responses to heat and photoperiod. *Crop Sci* 36:673–679. <https://doi.org/10.2135/cropsci1996.0011183X003600030026x>
- Eloward HO, Hall AE (1987) Influence of early and late nitrogen fertilization on yield and nitrogen fixation of cowpea under well-watered and dry field conditions. *Field Crop Res* 15:229–244
- FAOSTAT (2019) FAOSTAT, Statistical data base. Food and Agricultural Organization of the United Nations, Rome
- Fatokun C (2009) Designer (Cowpea) plants. Accessed on 16 Nov 2019 from <http://r4dreview.iita.org/index.php/2009/03/08/designer-cowpea-plants/>
- Fery RL (1980) Genetics of *Vigna*. In: Janick J (ed) *Horticultural reviews*. AVI Publishing, Westport, pp 311–394
- Fery RL (1985) The genetics of cowpea. A review of the world literature. In: Singh SR, Rachie KO (eds) *Cowpea research, production and utilization*. Wiley, Chichester, pp 25–62
- Fery RL, Singh BB (1997) Cowpea genetics: a review of recent literature. In: Singh BB, Mohan Raj DR, Dashiell KE, Jackai LEN (eds) *Advances in cowpea research*. Co-publication of IITA and JIRCAS, IITA, Ibadan/Tsukuba, pp 13–29
- Fery RL, Dukes PD, Cuthbert FP Jr (1977) Yield loss of southern pea (*Vigna unguiculata*) caused by *Cercospora* leaf spot. *Plant Dis Rep* 61(9):741–743
- Gamborg OL, Miller RA, Ojima K (1968) Nutrient requirements of suspension cultures of soybean root cells. *Exp Cell Res* 50:151–158
- Gomes AMF, Nhantumbo N, Pinto MF, Massinga R, Ramalho JC, Barros AR (2019) Breeding elite cowpea [*Vigna unguiculata* (L.) Walp] varieties for improved food security and income in Africa: opportunities and challenges. *Conference Proceedings. Intech Open*. <http://dx.doi.org/10.5772/intechopen.84985>
- Green SK (1991) Guidelines for diagnostic work in plant virology. AVRDC technical bulletin, vol 15. AVRDC, Taipei
- Hazra P, Chattopadhyaya A, Dasgupta T, Kar N, Das PK, Som MG (2007) Breeding strategy for improving plant type, pod yield and protein content in vegetable cowpea (*Vigna unguiculata*). *Acta Hort* 752:275–280
- Hitiksha KP, Acharya RR, Patel SR (2014) Interrelationship among green pod yield and its yield contributing characters and biochemical characters vegetable cowpea [*Vigna unguiculata* L. (Walp.)]. *Trends Biosci* 7(23):3972–3976
- Khalid II, Elharadallou SB (2013) Functional properties of cowpea (*Vigna unguiculata* L. Walp), and Lupin (*Lupinus termis*) flour and protein isolates. *J Nutr Food Sci* 3:1–6
- Kirse A, Karklina D (2015) Integrated evaluation of cowpea (*Vigna unguiculata* (L.) Walp.) and maple pea (*Pisum sativum* var. *arvense* L.) spreads. *Agron Res* 13:956–968
- Klopez (2009) Is genetically modified cowpea safe? Available from <http://r4dreview.iita.org/index.php/2009/03/08/640/>. Accessed 16 Nov 2019
- Kumar K, Dahiya SB, Rish N (1994) Inheritance to cowpea yellow MOSAIC virus in cowpea (*Vigna unguiculata* (L.) Walp.). In: Rishi N, Ahuja KL, Singh BP (eds) *Virology in the tropics*. Malhotra Publishing House, New Delhi

- Lachyan TS, Desai SS, Dalvi VV (2016) Inheritance study of qualitative and quantitative characters in cowpea varieties (*Vigna unguiculata* (L.) Walp.). *Electron J Plant Breed* 7(3):708–713. <https://doi.org/10.5958/0975-928X.2016.00091.0>
- Liyanage R, Perera OS, Wethasinghe P, Jayawardana BC, Vidanaarachchi JK, Sivaganesan R (2014) Nutritional properties and antioxidant content of commonly consumed cowpea cultivars in Sri Lanka. *J Food Legum Indian J Pulses Res* 27:215–217
- Lonardi S, Amatriain MM, Liang Q, Shu S, Wanamaker SI, Lo S, Tanskanen J, Schulman AH, Zhu T, Luo MC, Alhakami H, Ounit R, Hasan AM, Verdier J, Roberts PA, Santos JRP, Ndeve A, Dolezell J, Vrana J, Hokin SA, Farmer AD, Cannon SB, Close TJ (2019) The genome of cowpea (*Vigna unguiculata* [L.] Walp.). *Plant J* 98:767–782
- Lopes FCC, Gomes RLF, Filho FRF (2003) Genetic control of cowpea seed sizes. *Sci Agric* 60(2):315–318. <https://doi.org/10.1590/S0103-90162003000200016>
- Lopez K (2019) News crop: Cowpea. <https://www.iita.org/news-crop/cowpea/>
- Lucas M R, Diop N N, Wanamaker S, Ehlers J D, Roberts P A and Close T J (2011) Cowpea-soybean synteny clarified through an improved genetic map. *Plant Genome* 4: 218–224. <https://doi.org/10.3835/plantgenome2011.06.0019>
- Marechal R, Mascherpa JM, Stainer F (1978) Etude taxonomique d'un groupe complexe d'especes des genres *Phaseolus* et *Vigna* (Papilionaceae) sur la base de donnees morphologiques et polliniques, traitees par l'analyse informatique. *Boissiera* 28:1–273
- Melton A, Ogle WL, Barnett OW, Caldwell JD (1987) Inheritance of resistance to viruses in cowpeas. *Phytopathology* 77:642. (Abstract)
- Mithen R and Kibblewhite H (1993) Taxonomy and ecology of *Vigna unguiculata* (Leguminosae-Papilionoideae) in South Central Africa. *Kirkia* 14(1):100–113
- Mohammed BS, Ishiyaku MF, Abdullahi US, Katung MD (2015) Genetics of *cryIab* transgene in transgenic cowpea. *Prod Agric Technol* 11(1):108–116
- Moose SP, Mumm RH (2008) Molecular plant breeding as the foundation for 21st century crop improvement. *Plant Physiol* 147:969–977
- Muchero W, Diop NN, Bhat PR et al (2009) A consensus genetic map of cowpea *Vigna unguiculata* (L.) Walp. and synteny based on EST derived SNPs. *Proc Natl Acad Sci U S A* 106:18159–18164
- Muchero W, Roberts PA, Diop NN, Drabo I, Cisse N, Close TJ, Muranaka S, Boukar O, Ehlers JD (2013) Genetic architecture of delayed senescence, biomass, and grain yield under drought stress in cowpea. *PLoS ONE* 8:e70041
- Mudryj AN, Yu N, Hartman TJ, Mitchell DC, Lawrence FR, Aukema HM (2012) Pulse consumption in Canadian adults influences nutrient intakes. *Br J Nutr* 108:27–36
- Munoz-Amatriain M, Mirebrahim H, Xu P, Wanamaker SI, Luo M, Alhakami H, Alpert M, Atokple I, Batiemo BJ, Boukar O, Bozdag S, Cisse N, Drabo I, Ehlers JD, Farmer A, Fatokun C, Gu YQ, Guo YN, Huynh BL, Jackson SA, Kusi F, Lawley CT, Lucas MR, Ma Y, Timko MP, Wu J, You F, Barkley NA, Roberts PA, Lonardi S, Close TJ (2017) Genome resources for climate-resilient cowpea, an essential crop for food security. *Plant J* 89:1042–1054
- Murashige T, Skoog F (1962) A revised medium for rapid growth and bioassays with tobacco tissue cultures. *Physiol Plant* 15:473–497. <https://doi.org/10.1111/j.1399-3054.1962.tb08052.x>
- Mustapha Y, Singh BB (2008) Inheritance of pod colour in cowpea (*Vigna unguiculata* (L.) Walp.). *Sci World J* 3(2):39–42
- OECD (2016) Cowpea (*Vigna unguiculata*). In: Safety assessment of transgenic organisms in the environment, Volume 6: OECD consensus documents. OECD Publishing, Paris
- Ofuya TI (1987) Susceptibility of some *Vigna* species to infestation and damage by *Callosobruchus maculatus* (F.). *J Stored Prod Res* 23:137–138
- Ombakho GA, Tyagi Ap, Pathak RS (1987) Inheritance of resistance to the cowpea aphid in cowpea. *Theror Appl Genet* 74:817–819
- Orawu M, Melis R, Laing M, Derera J (2013) Genetic inheritance of resistance to cowpea aphid-borne mosaic virus in cowpea. *Euphytica* 189:191–201. <https://doi.org/10.1007/s10681-012-0756-3>

- Ouattara S, Chambish OL (1991) Inheritance of resistance to blackeye cowpea mosaic virus in “White acre-BVR” cowpea. *HortScience* 26:194–196
- Padulosi S (1993) Genetic diversity, taxonomy, and ecogeographic survey of the wild relatives of cowpea (*Vigna unguiculata* (L.) Walpers). Thesis, University Catholique de Louvain-La-Neuve, Louvain
- Padulosi S, Ng NQ (1997) Origin, taxonomy and morphology of *Vigna unguiculata* (L.) Walp. In: Singh BB, Mohan-Raj DR, Dashiell KE, Jackai LEN (eds) *Advances in cowpea research*. Co-publication of International Institute of Tropical Agriculture (IITA) and Japan International Research Center for Agricultural Sciences (JIRCAS). IITA, Ibadan
- Palmer JL, Lawn RJ, Adkins SW (2002) An embryo-rescue protocol for *Vigna* interspecific hybrids. *Aust J Bot* 50:331–338
- Pandey RN, Dhanasekar P (2004) Morphological features and inheritance of foliaceous stipules of primary leaves in cowpea (*Vigna unguiculata*). *Ann Bot* 94:469–471. <https://doi.org/10.1093/aob/mch161>
- Pant KC, Chandel KPS, Joshi BS (1982) Analysis of diversity in Indian cowpea genetic resources. *SABRAO J* 14:103–111
- Pasquet RS (1993a) Classification infraspécifique des formes spontanées de *Vigna unguiculata* (L.) Walp. à partir des données morphologiques. *Bulletin du Jardin Botanique National de Belgique* 62(1/4):127–173. <https://doi.org/10.2307/3668271>
- Pasquet RS (1993b) Two new subspecies of *Vigna unguiculata* (L.) Walp. *Kew Bull* 48:805–806
- Pasquet RS (1997) A new subspecies of *Vigna unguiculata*. *Kew Bull* 52(4):840. <https://doi.org/10.2307/4117815>
- Pasquet RS (1998) Morphological study of cultivated cowpea *Vigna unguiculata* (L.) Walp. Importance of ovule number and definition of cv. gr *Melanophthalmus*. *Agronomie* 18(1): 61–70. <http://dx.doi.org/10.1051/agro:19980104>
- Pasquet R S (1999) Genetic relationships among subspecies of *Vigna unguiculata* (L.) Walp. based on allozyme variation. *Theoretical and Applied Genetics* 98 (6): 1104–1119
- Patel PN (1981) Pathogen variability and host resistance to three races of the bacterial pustule pathogen in cowpea. *Trop Agric (Trinidad)* 58:275–280
- Patel PN, Mligo JK, Leyna HK, Kuwait C, Mmbaga ET (1982) Source of resistance, Inheritance and breeding of cowpea for resistance to a strain of cowpea aphid-born mosaic virus from Tanzania. *Indian J Genet* 42:221–229
- Pathak RS (1988) Genetics of resistance to aphid in cowpea. *Crop Sci* 28:474–476
- Pathmanathan U, Rasiyah PA, Syed QH (1997) Genetic analysis of yield and its components in vegetable cowpea (*Vigna unguiculata* L. Walp). *Euphytica* 96(2):207–213
- Ponz F, Russell ML, Rowhani A, Bruening G (1988) A cowpeas line has distinct genes for resistance to tobacco ringspot virus and cowpea mosaic virus. *Phytopathology* 78:1124–1128
- Pottorff MO, Li G, Ehlers JD, Close TJ, Roberts PA (2014) Genetic mapping, synteny, and physical location of two loci for *Fusarium oxysporum* f. sp. *tracheiphilum* race 4 resistance in cowpea *Vigna unguiculata* (L.) Walp. *Mol Breed* 33:779–791
- Pradhan D, Mathew D, Mathew SK, Nazeem PA (2018) Identifying the markers and tagging a leucine-rich repeat receptor-like kinase gene for resistance to anthracnose disease in vegetable cowpea [*Vigna unguiculata* (L.) Walp.]. *J Hort Sci Biotechnol* 93(3):225–231
- Raveendar S, Premkumar A, Sasikumar S, Ignacimuthu S, Agastian P (2009) Development of a rapid, highly efficient system of organogenesis in cowpea *Vigna unguiculata* (L.) Walp. *S Afr J Bot* 75:17–21
- Rodrigues MA, Santos CAF, Santana JRF (2012) Mapping of AFLP loci linked to tolerance to cowpea golden mosaic virus. *Genet Mol Res* 11(4):3789–3797
- Rusoke DG, Fatunla T (1987) Inheritance of pod and seed resistance to the cowpea seed beetle (*Callosobruchus maculatus* Fabr.). *J Agric Sci (Camb)* 108:655–660
- Sangwan SR, Rish N (2004) Genetics of resistance to cowpea yellow mosaic virus in cowpea (*Vigna unguiculata* (L.) Walp.). *Indian J Mycol Plant Pathol* 34:620–622

- Santos AAD, Freire-Filho FR (1984) Reducao da producao do feijao massacar causado pelo vírus do mosqueado amarelo. *Fitopatol Bras* 9:407
- Schneider RW, Williams RJ, Sinclair JB (1976) Cercospora leaf spot of cowpea: models for estimating yield loss. *Phytopathology* 66:384–388
- Sebetha ET, Modi AT, Owoeye LG (2014) Cowpea crude protein as affected by cropping system, site and nitrogen fertilization. *J Agric Sci* 7:224–234
- Singh B B, Chambliss O L, Sharma B (1997). Recent advances in cowpea. In: Singh B.B., Mohan-Raj D.R., Dashiel K.E., Jackai L.E.N. (Eds.). *Advances in cowpea research*. Co-publication of International Institute of Tropical Agriculture (IITA) and Japan International Research Center for Agricultural Sciences (JIRCAS), Ibadan, Nigeria 30–49
- Singh BB (2002) Recent genetic studies in cowpea. In: Fatokun CA, Tarawali SA, Singh BB, Kormawa PM, Tamo M (eds) *Challenges and opportunities for enhancing sustainable cowpea production*. Proceedings of the World cowpea conference III held at the International Institute of Tropical Agriculture (IITA), Ibadan, 4–8 Sept 2000. IITA, Ibadan, pp 3–13
- Singh DB, Reddy PP (1986) Inheritance of resistance to root-knot nematode in cowpea. *Indian J Nematol* 16:284–285
- Singh BB, Singh SR (1985) Breeding for bruchid resistance in cowpea. In: Fujii K, Gatehouse AMR, Johnson CD, Mitchel R, Yoshida T (eds) *Bruchids and legumes: economics, ecology and coevolution*. Proceedings of the second international symposium on bruchids and legumes (ISBL-2) held at Okayama, 6–9 Sept 1989
- Singh BB, Singh SR, Adjadi O (1985) Bruchid of resistance in cowpea. *Crop Sci* 25:736–739
- Singh J, Kalloo G, Singh KP (2001) Vegetable crops: nutritional security. Indian Institute of Vegetable Research, Varanasi, p 56
- Smartt J (1990) The old world pulses: *Vigna* species. In: *Grain legumes: evolution and genetic resources*. Cambridge University Press, Cambridge, pp 140–175
- Somers DA, Samac DA, Olhoft PM (2003) Recent advances in legume transformation. *Plant Physiol* 131:892–899
- Sousa LL, Cruz AS, Vidigal Filho PS, Vallejo VA, Kelly JD, Gonçalves-Vidigal MC (2014) Genetic mapping of the resistance allele Co-52 to *Colletotrichum lindemuthianum* in the common bean MSU 7-1 line. *Aust J Crop Sci* 8:317–323
- Sousa LL, Gonçalves AO, Gonçalves-Vidigal MC, Lacanallo GF, Fernandez AC, Awale H, Kelly JD (2015) Genetic characterization and mapping of anthracnose resistance of common bean landrace cultivar Corinthiano. *Crop Sci* 55:1900–1910. <https://doi.org/10.2135/cropsci2014.09.0604>
- Subbiah A, Prabhu M, Rajangam J, Jagadeesan R, Anbu S (2013) Genetic analysis of vegetable cowpea [*Vigna unguiculata* (L.) Walp.]. *Legum Res* 36(1):1–9
- Timko MP, Rushton PJ, Laudeman TW, Bokowiec MT, Chipumuro E, Cheung F, Town CD, Chen X (2008) Sequencing and analysis of the gene-rich space of cowpea. *BMC Genomics* 9:103
- Trehan I, Benzoni NS, Wang AZ, Bollinger LB, Ngoma TN, Chimimba UK et al (2015) Common beans and cowpeas as complementary foods to reduce environmental enteric dysfunction and stunting in Malawian children: study protocol for two randomized controlled trials. *Trials* 16:520
- Verdcourt B (1970) Studies in the leguminosae-Papilionoideae for the ‘flora of tropical East Africa’: IV. *Kew Bull* 24(3):507–569. www.jstor.org/stable/4102859
- Winter S, Butgereitt A, Thottappilly G (2002) Cowpea golden mosaic virus and related geminiviruses associated with *Vigna* spp. in Nigeria. Poster presentation. Intern Virology Congress
- Yang H, Tao Y, Zheng Z, Li C, Sweetingham MW, Howieson JG (2012) Application of next generation sequencing for rapid marker development in molecular plant breeding: a case study on anthracnose disease resistance in *Lupinus angustifolius* L. *BMC Genomics* 13:318–328. <https://doi.org/10.1186/1471-2164-13-318>