



Understanding the Genetic Basis of Resistance to Cowpea Scab: Insights into Parental Combining Ability and Gene Action in Breeding Strategies

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ABSTRACT

Cowpea (*Vigna unguiculata*) is an essential leguminous crop with significant importance in global agriculture and food security. However, it is susceptible to various diseases, with Cowpea Scab (a fungal disease caused by *Sphaceloma* sp.) being a major constraint to its production. Breeding for resistance to Cowpea Scab is a crucial strategy to enhance cowpea productivity and reduce yield losses. This review paper examines the role of parental combining ability and gene action in breeding for resistance to Cowpea Scab. Parental combining ability of scab resistance has been evaluated on different cowpea germplasm and has shown that General Combining Ability (GCA) is more important than Specific Combining Ability (SCA) in the inheritance of scab resistance. The higher narrow sense heritability also signifies the contribution of additive genetic variability in scab resistance inheritance.

Keywords: cowpea, combining ability, heritability, genetic improvement, scab resistance

RÉSUMÉ

Le niébé (*Vigna unguiculata*) est une légumineuse essentielle, d'une grande importance pour l'agriculture mondiale et la sécurité alimentaire. Cependant, il est sensible à diverses maladies, la gale du niébé (une maladie fongique causée par *Sphaceloma* sp.) constituant un obstacle majeur à sa production. La sélection pour la résistance à la gale du niébé est une stratégie cruciale pour améliorer la productivité du niébé et réduire les pertes de rendement. Cet article de synthèse vise à examiner de manière approfondie le rôle de la capacité combinatoire parentale et de l'action des gènes dans la sélection pour la résistance à la gale du niébé. La capacité combinatoire parentale de la résistance à la gale a été évaluée sur différents germoplasmes de niébé, et il a été montré que la capacité combinatoire générale (GCA) est plus importante

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que la capacité combinatoire spécifique (SCA) dans l'héritabilité de la résistance à la gale. La forte héritabilité au sens étroit a également indiqué la contribution de la variabilité génétique additive dans l'héritabilité de la résistance à la gale.

Mots-clés: niébé, résistance à la gale, capacité combinatoire, héritabilité, amélioration génétique

INTRODUCTION

Cowpea (*Vigna unguiculata* L. Walp) is a vital crop for world agriculture and food security due to its significance agronomically, nutritionally and commercially. Cowpeas are a staple food for many people in Central America, Africa, Asia, and Southern America (Osipitan *et al.*, 2021). Nutritionally, the crop offers human consumption protein (Phillips *et al.*, 2003) as well as cattle feed (Singh *et al.*, 2003). Cowpeas also support the sustainability of agricultural systems through a symbiotic relationship with the root nodulating bacteria, thereby fixing nitrogen directly into the soil, thus enhancing crop development and grain productivity within the ecosystem (Singh *et al.*, 2003). This characteristic lowers the production expenses related to nitrogen fertilizer application. As a cover crop, it improves the fertility of the soil and suppresses weeds (Akasah *et al.*, 2023), in addition to reducing incidences of *Striga hermonthica*, when crop rotation including cowpea is practiced (Berner *et al.*, 1996).

The majority of the world's cowpea-producing nations are located in sub-Saharan Africa, or the Sudano-Sahelian vegetation region (Boukar *et al.*, 2019). Nigeria, Niger, and Burkina Faso have the highest production, according to FAOSTAT (2023). The production output per cultivated area of cowpeas across various countries is measured by productivity (Table 1). Around 14 million hectares are cultivated for cowpeas annually, with 7 million tons of dry grain harvested and the rest either consumed as animal fodder or as a vegetable. Africa is cowpea's primary producing region, accounting for 96.7% of global production (FAOSTAT, 2023). Because of the biotic and abiotic stresses that the crop faces, high yield are unlikely to be achieved. Cowpea scab disease is one of the most devastating biotic stress capable of causing 100% yield loss, if not controlled.

Scab of cowpea is a seed borne disease caused by *Sphaceloma* sp which is an anamorph of *Elsinoe phaseoli* in common bean (Bean scab). The disease infects every portion of the plant that is above ground, first as puckering of the lamina (Emechebe, 1980), within three to six days of infection and matures to white spots (1 × 2.5 mm) sometimes with brown borders. When the disease is severe, the leaf spots coalesce to larger lesions, giving the affected area a rough, deformed appearance. In some cases, the centers of these older spots could later fall out, causing shot holes.

The disease also infects the stems and peduncles, forming silver-grey oval and elongated lesions, with dark brown elliptical margins. When chlamydospores grow on the petioles, stem, peduncles, and pods, these spots turn dark brown (Emechebe, 1980). According to Singh and Allen (1979), infected pods have ovoid gray blotches with brown borders around them. In severe infestations, the pods may abort or stay attached to the plant as mummified black lumps devoid of seeds (Emechebe, 1980; Emechebe and Shoyinka 1985). According to Omoigui *et al.* (2020), high infection levels cause undersized plants, heavily marked leaves, stems, and pods, as well as leaves, flowers, and pods that fall off before they ripen. Such high disease intensity may also cause flower axis injury resulting in either flower and/or pod abortion or total flower formation prevention. Scab therefore causes a reduction in seed production and viability, as well as in pod size and number (Nakawuka and Adipala, 1997). Nonetheless, it has been noted that peduncles that flower following the cessation of the rains may produce normal-sized, healthy pods (Emechebe, 1980). Scab on young leaves in its early stages resembles cowpea mosaic viruses symptomatically; nevertheless, on pods and stems, it can be mistaken for anthracnose caused by *Colletotrichum lindemuthianum* (Sacc. and Magn.) Bri. and CavT (Emechebe, 1980).

Table 1. Production and productivity of cowpea in selected countries in the world

S/N	Country	Production in tons	Yield per hectare	Area harvested	Inference on production	Inference on productivity	Continent
1	Nigeria	2,606,912	9,137	2,853,097	1st	7th	Africa
2	Niger	2,376,727	4,035	5,889,677	2nd	18th	Africa
3	Burkina Faso	630,965	4,826	1,307,336	3rd	12th	Africa
4	Ghana	215,350	19,862	11,898	4th	2nd	Africa
5	Tanzania	202,865	4,096	30,366	5th	6th	Africa
6	Cameroon	185,832	4,043	258,898	6th	9th	Africa
7	Kenya	179,399	4,367	11,154	7th	10th	Africa
8	Mali	157,739	3,767	160,412	8th	11th	Africa
9	Myanmar	136,411	11,425	119,398	9th	4th	Asia
10	Sudan	104,667	2,678	333,638	10th	17th	Africa
11	Mozambique	89,356	5,545	284,451	11th	20th	Africa
12	Democratic Republic of Congo	72,726	4,432	95,803	12th	15th	Africa
13	Senegal	60,422	6,889	260,408	13th	19th	Africa
14	Malawi	42,456	13,515	159,345	14th	13th	Africa
15	United States	23,632	4,296	169,279	15th	1st	North America
16	China	15,652	8,876	209,371	16th	5th	Asia
17	Madagascar	13,000	8,907	14,596	17th	8th	Africa
18	Uganda	12,439	9,750	208,059	18th	16th	Africa
19	Sri Lanka	11,180	11,770	9,499	19th	3rd	South Asia
20	South Africa	4,871	10,360	15,108	20th	14th	Africa

Data from Omomowo and Babalola (2021)

Significance of Cowpea Scab in cowpea production.

Cowpea scab has been reported to be common throughout tropical Africa and is the most devastating disease in areas where Cowpea is grown including Brazil, Central America, and the northern and southern Guinea savanna zones of West and Central Africa (Emechebe and Shoyinka, 1985; Lin and Rios, 1985; Mbong *et al.*, 2010). In the Eastern and Southern regions of Africa, the disease is widespread in Uganda, Tanzania, Kenya, Ethiopia, Zambia and Rwanda (Iceduna, 1994; Edema *et al.*, 1996; Tumwegamire *et al.*, 1998; Afutu *et al.*, 2017). Despite its wide geographical distribution, the disease is most prevalent in semi-arid agro ecological environments (Mbong *et al.*, 2010).

In severe infections, the disease can cause yield reductions as high as 100% in Savannah areas (Mbong *et al.*, 2010) as reported in Uganda (Iceduna *et al.*, 1994; Tumwegamire *et al.*, 1998) and Nigeria (Emechebe and Shoyinka, 1985; Mungo *et al.*, 1995). The disease can cause reductions in grain yield directly or indirectly through deleterious effects on its yield components (Tumwegamire *et al.*, 1998; Mbong *et al.*, 2010). Scab disease caused 70% losses in grain production and total crop loss in Kachia (Emechebe, 1980) in the northern Guinea savanna of Nigeria (Zaria) in 1989 and 1990 (Mungo *et al.*, 1995). In another study carried out to show the effect of scab on grain yield in Northern Nigeria, of the three varieties

studied, Variety TVx 3236 showed inconsistent correlation between scab infected plant parts with grain yield and yield components (Mbong *et al.*, 2010). This variety had the least scab infection thus contributing only 13.7%-29.5% grain yield reduction. TVx 3236 displayed no direct and indirect, percent individual and combined contributions of scab infection on the leaves in 2004, 2005 and 2006. Contribution of scab infection to grain yield by Variety SAMPEA-6 ranged from 41.3-66.9% and variety IT93K452's range was 35.9%-67.1%. As per the findings, cowpea grain output was either directly or indirectly decreased by scab-infected plant parts of the susceptible varieties. This meant that if the disease is not controlled, this would yield by as much as 67%. The study therefore suggested that, in the conditions of northern Nigeria, the usage of resistant varieties could reduce scab infections.

Similarly, in Uganda, grain yield was shown to be negatively correlated with foliar scab both directly ($r = 0.588$) and indirectly by reducing number of pods per plant ($r = -0.195$) and pod length ($r = -0.243$). Similarly, pod scab severity also indirectly reduced grain yield by negative correlation with pods per plant ($r = -0.330$) and pod length ($r = -0.175$) (Tumwegamire *et al.*, 1998). This confirmed that scab severity reduces grain yield through its direct and indirect deleterious effects on the above yield components. Although Uganda's mean cowpea yield has been reported to be less than 400 kg ha⁻¹, (Omongo *et al.*, 1997), an output potential of 3000 kg/ha⁻¹ was stated to be attainable by Rusoke and Rubaihayo (1994), with a yearly cowpea production expected to be 20,000 tons.

Factors that affect Cowpea Scab distribution

Scab disease development is favored by moderate temperatures between 23 and 28 degrees Celsius, along with high relative humidity, with its principal sources of inocula as contaminated seed and infested plant debris (Allen, 1983). Emechebe and Shoyinka (1985) further added that the secondary dispersion agents of the fungal conidial inoculum are wind-driven moisture and rain splash. Studies have reported that Scab disease development is favoured in conditions of high relative humidity and precipitation than during the dry periods (Nakawuka and Adipala, 1997; Emechebe, 1980). However, Iceduna *et al.*

(1994) observed that there was more disease during dry conditions in Uganda.

In a study conducted in Uganda to assess the prevalence, severity, and distribution of scab disease in 17 cowpea growing regions, it was shown that scab occurrence and infection lead was influenced by altitude (Afutu *et al.*, 2017). The higher altitudes could have led to higher relative humidity thus favouring long periods of leaf surface wetness, which have been reported to favour the development and sporulation of fungal diseases. The districts that recorded the greatest mean disease incidence (82%) and severity (3.4) were those that were situated above 1200 meters above sea level, whereas those that lie on mean altitudes ranging between 894 and 1221 metres above sea level (m.a.s.l) showed scab with mean disease incidence ranging between 35-70%. The lowest scab incidence (64.7%) and severity score (2.7) was observed in areas situated on lower altitudes, between 771 and 990 m.a.s.l.

Incidence and severity were also affected by the choice of seed source and long-term use of a particular cultivar. The cowpea genotypes Sunshine, WC 36, and WC 29 (West *et al.*, 2001) that have been proven to be susceptible to scab were the predominant ones grown in the Tororo and Amuria districts throughout the study (Afutu *et al.*, 2017). This explains the increased frequency and severity of scab in those regions and may be the result of pathogens adapting to those environments. Nonetheless, in both years, districts Yumbe, Arua, and others continuously registered comparatively lower incidences and severities. This was due to observations that the predominant cultivar in these districts is Alegi, which has been shown to have a reasonable level of disease resistance.

Control of cowpea scab

A number of strategies have been applied in the control of *Sphaceloma* scab to avoid the possibility of it becoming an epidemic.

Sanitation and crop rotation. Given that contaminated crop debris is a major source of scab disease (Emechebe, 1980) and that the fungus is highly specialized in *Vigna unguiculata*, crop rotation and sanitation would be appropriate measures to

reduce the disease. According to [Sivanesan and Holiday \(1971\)](#), sanitation was also recommended as a means of managing Lima bean scab. [Mungo et al. \(1995\)](#) demonstrated that in the use of crop rotation, scab symptoms were less severe in fields where cowpea followed another crop in rotation than in those where cowpea followed cowpea. Here, the rotation of rotation Crop has an effect on the occurrence of scabs.

Cropping system. The effect of intercropping in reducing pest and disease incidence has been reported by [Mukiibi, \(1976\)](#), and this explains its active implementation in subsistence farming ([Adipala et al., 1999](#)). On the other hand, [Afutu et al. \(2016a\)](#) conducted a study that examined the impact of cropping system and past crop history on the incidence of scab disease in 17 districts in Uganda. According to the research, the average occurrence of scab disease observed in fields with intercropping was considerably more ($P < 0.05$) than that in fields with monocropping. This also depended on the type of crops being intercropped. Fields that were intercropped with cassava and legumes had higher scab incidence and severity compared to fields that had been planted with cereal and other root crops ([Afutu et al., 2017](#)). These two crops are affected by different forms of scab fungi; *Sphaceloma manihoticola* for cassava and *Elsinoë phaseoli* for common beans; these could have led to cross infection of these scab fungi from the two crops to the cowpea crops ([Afutu et al., 2017](#)).

Similarly, [Mbong et al. \(2016\)](#), used a cowpea variety (Ife brown) susceptible to scab disease and two varieties of cereals (sorghum, ICSVIII-extra early and maize, TZEEW-extra early) to study the effect of scab disease on the yield of intercrop systems of cowpea, maize and sorghum. Five intercropping patterns that is: intra- row, inter-row, double-row, strip cropping for maize: cowpea and sorghum: cowpea, were compared to sole cowpea cropping. Results showed that sole cropped cowpea had a higher yield than these under intercropping cropping systems. Since previous studies have indicated that scab reduces yield ([Tumwegamire et al., 1998](#)), a higher yield observed could mean that the sole cowpea pattern was less infected with scab disease than in other inter cropping systems.

Biological control. Use of formulations of *Trichoderma harzianum*, *Pseudomonas fluorescens* and *Bacillus cereus* was recommended in the management of fungal diseases of cowpea and groundnut. These formulations were applied as foliar spray, seed treatment and were also incorporated into the soil through broadcasting. The study took place at the Institute for Agricultural Research farms, at Samaru, Zaria, in Minjibir, Kano in the Sudan savanna and in the Northern Guinea savanna. Results showed that there was disease reduction of up to 54%, thus recommending the use of biological formulations in the soils of Nigerian savanna in the control of fungal diseases in legumes ([Yakubu et al., 2019](#)).

Chemical control. Both foliar-applied fungicides and fungicidal seed treatment have proven effective methods of controlling scab ([Mungo et al., \(1995\)](#)). A study by [Mungo et al., \(1995\)](#), showed that applying different frequencies and concentrations of a fungicide such as benomyl (**Benlate 50 WP**) can reduce cowpea scab at different disease phases. Using cowpea varieties, IT 84S-2140 and IT 85F-1517 that are susceptible to *Sphaceloma* scab but resistant to several other diseases of cowpea, including brown blotch (*Colletotrichum cupsici*), bacterial blight (*Xanthomonas campestris* pv. *vignicolu*) and Septoria leaf spot (*Septoria vignae*), different disease levels were generated by applying benomyl at the rate of 0.6 kg /400 litres of water at 4-, 7-, 14-, 21-, 28-, or 35-day intervals. Plots sprayed at four days interval recorded the least disease severity (25%), compared to the 71% crop loss at 35 days interval. The results indicated that spraying benomyl weekly at 0.5 kg/400 litres can reduce crop loss by preventing flowers abscission and reducing severity of pod scab.

In another study, the fungicide sprays of mancozeb (dithane-M45) at 30 g/15l and benomyl (benlate), sprayed at a rate of 15 g/15l, considerably decreased scab attack during the first and second rains, as demonstrated by [Edema and Adipala \(1996\)](#). Furthermore, when cowpea seeds were treated with biological formulations of *Trichoderma harzianum*, *Pseudomonas fluorescens* and *Bacillus cereus*, a chemical spray, Funguforce (Mancozeb + Carbendazimin) and a control, lowest rates of scab disease were recorded by Funguforce at 10% at Minjibir, Kano and 8.5% at Institute for Agricultural

Research located at Samaru in Sudan (Yakubu *et al.*, 2019). However, due to the dangers in pesticide use and the lack of knowledge for using pesticides efficiently, the use of host resistant varieties is the most effective way to scab and its control economic losses (Rusoke and Rubaihayo, 1994; Mbong *et al.*, 2012).

Host Resistance to Scab Disease

Traditional breeding approaches. Plant resistance is the use of resistant crop varieties, alone or in combination with other strategies to reduce the effect of biotic and abiotic stresses on crop productivity (Stout, 2014). Breeding for resistance involves the use of genetic resources to increase a plant's resilience to biotic and abiotic challenges. Two methods are used in plant breeding to obtain disease resistance as a factor of crop improvement: Conventional breeding and marker-assisted breeding (MAB) (Breseghello and Coelho, 2013). In conventional breeding, traditional breeding techniques are used, where the genetic resources are screened for resistance or tolerance to biotic and abiotic stresses (Stout, 2014), the best performing ones selected and mated as parents, and the best performing progeny are then phenotypically selected across a number of generations (5–12 years) (Bhat *et al.*, 2016).

Understanding the genetic diversity of plant germplasm has been vital in improving different traits in plants (Ali *et al.*, 2007). According to Onda and Mochida (2016), diversity can result in beneficial traits that aid in resolving issues related to food security. Genetic diversity refers to the proportion of diversity of numerous traits present in different genotypes of the same species (Bhandari *et al.*, 2017). In breeding, genetic diversity is estimated by measuring either the amount of phenotypic variation of quantitative and qualitative traits, or the genotypic variation, which is majorly DNA-based and allozymes (allelic variants of enzymes) (Holderegger *et al.*, 2006). It is however worth-noting that the total phenotypic variation is a contribution of the genetic composition, environment, and interactions between the plant and its environment (Vogt, 2020). Genetic diversity in a population promotes the efficient use of genetic variation in crop germplasm in selection of superior performing genotypes and development of new and improved cultivars with particular desirable attributes (Bhandari *et al.*, 2017). Genetic variation is

the quantity of the genetic differences that occur within a population. It arises from any changes in a population's genetic makeup, for example, due to sexual reproduction, gene flow, or mutations (Terfa and Gurmu, 2020). These sources of variation cause different genotypes by altering, adding, or removing alleles from a species' population (Chung *et al.*, 2023). Genetic variation is a key component of genetic diversity because it increases the population's adaptability to environmental changes, thus avoiding the risk of extinction (Terfa and Gurmu, 2020). The degree of genetic variability and heritability of the desired trait determine the quantity of crop improvement (genetic gain) of that trait (Jafari *et al.*, 2017).

Genetic Diversity in cowpea. High phenotypic and genetic diversity of cowpea genotypes is observed in Sub-Saharan Africa, primarily in East and Central Africa (Boukar *et al.*, 2019). The majority of cowpea varieties that are weedy and wild come from the subregion of southern and eastern Africa (Coulibaly *et al.*, 2002), whereas the cultivated varieties are more widely found in West Africa (Ng and Maréchal, 1985). In a study by Huynh *et al.* (2013), a set of more than 1200 SNP markers was used to genotype a worldwide collection of 422 cowpea landraces and African ancestral wild cowpea. Results showed that the total genetic variation within landraces from Africa (3%) was less than that from countries outside Africa (69%). The local landraces in America were genetically distinct from those of other global regions, like Oceania and East Asia. Also, according to Fatokun *et al.* (2018), there is a considerable genetic similarity between the African accessions and the American breeding lines, but there is also a likeness between the West African, Asia and European accessions (Huynh *et al.*, 2013).

Genetic Diversity of Cowpea Scab

Genetic variability and heritability of Cowpea Scab Resistance. Variability of this *Sphaceloma* sp fungus was shown in different studies where local and elite germplasm were screened for sources of resistance to the scab disease. In Uganda, host resistance studies on cowpea scab were initiated by Takan *et al.* (1988). In Zambia, of the 210 cowpea lines screened for host resistance to various diseases, none was completely free of scab, but only five, that

were moderately resistant (Kannaiyan *et al.*, 1987). According to Iceduna *et al.* (1994), research on eighty cowpea lines revealed that scab severity varied with season, with 32% infection in 1991, and 2% and 24% infection in the first and second seasons of 1992. Lines 46, 39, Kvu 145, and Kvu 454 were resistant to scab. Additional screening of 75 cowpea lines for sources of scab resistance revealed that 35 lines were susceptible, 10 lines resistant and 30 were moderately resistant to foliar infection. The most resistant lines were 46, Majije Ex2, IT82D-3850-1, KATUMANI 80, 17, 39, IT82D-716, and KVu/175 (Nakawuka and Adipala, 1997). For pod scab, 11 lines were susceptible, 24 lines resistant, and 40 of the lines were either moderately resistant or susceptible. Of the resistant lines, only KVu/175, 39 and 46 maintained high levels of resistance to *Sphaceloma* scab.

Evaluation of 100 cowpea lines in two locations; Makerere University Agricultural Research Institute (MUARIK), Kabanyolo, Central Uganda (humid region) and the National Semi Arid Resources Research Institute (NaSARRI) Serere, Uganda, (Semi-arid region) showed variability in their response to scab, where lines that were resistant in one location, were susceptible in another. This suggested the presence of different pathotypes of scab (Afutu *et al.*, 2016), which complicates crop protection initiatives (Alvarez *et al.*, 2003). These studies emphasize the need to breed for stable and durable resistant cultivars. Similarly, Konate and Ouedraogo (1988) also reported that TVx 3236 variety was susceptible to scab in Burkina Faso yet resistant in Nigeria, thus signifying the existence of at least two races of the pathogen in West Africa.

Three hundred ninety (390) improved cowpea genotypes for resistance to scab disease and yield also showed a significant variation among genotypes and seasons and for genotypes by seasons interactions (Alipa, 2023). The study recommended cowpea genotypes; TVU-2968, SanZi, 1195K-1093-5-A, TVU-15114, and Taef-14-inhaca.E for use as parents in breeding for scab resistance.

Genetic variation in *Sphaceloma* sp. has been shown using molecular markers, such as Random Amplified Polymorphic DNA (RAPD) molecular markers. These were used in the characterization of

Sphaceloma manihoticola isolates in Brazil (Alvarez *et al.*, 2003) and in delimiting species among *Elsinoe* isolates (MChau *et al.*, 1998). In Uganda, Afutu *et al.* (2016) used nine Inter-Simple Sequence Repeat (ISSR) markers in determining the genetic variability and relationships among 86 isolates from 14 populations of the scab fungus obtained from different geographical regions of Uganda. A total of 311 polymorphic loci obtained were acquired from the PCR amplifications of these isolates. Results of the Analysis of molecular variance also showed that there was 96% genetic variation within the populations, 4% among the populations but no genetic variation among the different regions. The results therefore indicated that there could be a form of interaction occurring among regions and yet a low gene flow across all populations (Afutu *et al.*, 2017).

Genetics of Cowpea Scab Resistance

Plant disease resistance can be broadly classified into resistance traits that are quantitative and those that are qualitative. For quantitative disease resistance, numerous minor-effect genes spread across different loci and their combined influence on the phenotype is additive (Rutkoski *et al.*, 2016). The inheritance of a quantitative resistance trait is dependent on many genes from the different loci (Niks *et al.*, 2015). This type of resistance works by delaying the progression of the disease through lengthening the latency period and other epidemic-related factors. Qualitative disease resistance is controlled by single genes; these

exist as different alleles or in groups at some loci in the genome, conferring resistance towards only active against particular races of the pathogen (Keller *et al.*, 2000). Both types of resistance are important in breeding. However, because quantitative disease resistance is more durable compared to qualitative disease resistance, breeders primarily target this type of resistance (Wang *et al.*, 2023). This underlying genetic basis of a phenotype is termed as the genetic architecture of that trait. This term explains how genes and environmental factors interact to create phenotypes (Fu *et al.*, 2013). It could therefore include the quantity of quantitative trait loci (QTL) that influence individual variation in the trait, their effect sizes, the frequency of additive, dominant, or recessive alleles for causative polymorphisms in the

population, patterns of gene-gene and gene-environment effects, and degrees of pleiotropy (Mackay, 2001). The genetics of quantitative resistance of agricultural traits and quantitative trait loci have been determined majorly by the use of molecular markers (Keller *et al.*, 2000).

Combining Ability and gene action. In developing disease resistant and high-yielding genotypes, the existing germplasm is screened for those traits, followed by selection of the best genotypes to be used as parents (Mansour *et al.*, 2018). During hybridization of the parents, the type and magnitude of gene action regulating the expression of quantitative traits is then determined (Falconer, 1989). This information is provided by combining ability studies (Sunny *et al.*, 2022). Combining ability is the effectiveness of parental lines in producing hybrids and is determined by the type of gene action controlling the trait of interest (Nduwumuremyi *et al.*, 2013). In these studies, parental combinations with high specific combining (SCA) and high General Combining Ability (GCA) are identified. General combining ability is used to determine the general performance of the parents and is due to additive effects and additive \times additive interactions. The specific combining ability effect denotes hybrid performance by identifying loci with dominant gene activity (non-additive effects) and all other components of epistatic interactions (additive \times dominance and dominance \times dominance interactions).

Reliable information regarding the general and specific combining capabilities of parents and their cross combinations can be obtained by both Diallel (Griffing, 1956; Kamara *et al.*, 2021) and line \times tester (Kempthorne, 1956) mating designs. In order to predict the parents' combining ability, a mating design known as full diallel analysis crosses specific parents in every possible way (Fasahat *et al.*, 2016). Diallel cross is important in analyzing continuous variations among the genotypes in a balanced and systematic way (Bhattacharjee and Sarkar, 2018). In these mating designs, breeders are interested in discovering how significant the genetic variation is; the amount of the variation that is heritable; the types of gene affecting that significance. Plants with superior genotypes, are identified based on the combining ability effects with

better mean performance (Nduwumuremyi *et al.*, 2013).

Gene Action in Cowpea Scab Resistance. The gene action of scab resistance was studied by Nakawuka and Adipala (1997), where five lines selected based on their resistance levels were crossed in a diallel mating design, in order to determine the pattern of inheritance of scab resistance (Griffing, 1956). Assessment of the general combining abilities (GCA) of the parents and specific combining abilities (SCA) of the crosses concluded the GCA was of greater importance than SCA in inheritance of scab resistance. Results showed higher GCA mean square, which was 6.4 times larger than the SCA mean squares. Lines 39 and 46 had the highest negative general combining ability (GCA) of -0.55 and -0.36, respectively, thus suggesting a high gene frequency for scab resistance (Nakawuka and Adipala, 1997). According to these findings, scab resistance is mostly controlled by additive gene action. This type of gene action is a form of quantitative resistance and non-race-specific resistance (Wang *et al.*, 2023). The GCA reflects additive gene action, while SCA is non-additive gene action (Chen *et al.*, 2019). In order to increase cowpea resistance to scab, resistant sources would make excellent parents.

In another study on the genetics of resistance to *Sphaceloma* scab of cowpea by Tumwegamire *et al.* (1998) among 10 cowpea parents which were crossed according to Griffing, (1956) method, the effects of both General Combining Ability (G.C.A) and Specific Combining ability (S.C.A) were vital for resistance to both foliar and pod scab infection. This signified that both additive and non-additive gene actions are important for scab resistance. The study further showed a high ratio of G.C.A: S.C.A (37.2 and 35.8) for foliar and pod scab severities, respectively, thus indicating a majority of additive genetic variance for each trait. These findings are in agreement with those of Nakawuka and Adipala (1997). Furthermore, the high Narrow-sense heritability estimates, 79.8% and 84.5%, for foliar and pod scab, respectively, also indicated a high proportion of the additive genetic variance attributable to the observed phenotypic variance (Falconer, 1989; Tumwegamire *et al.*, 1998). Additive gene action (the total effects of multiple genes contributing to a single phenotype) is the

quantity of genetic variation in a population, that is captured by the narrow sense heritability (Wray and Visscher, 2008). Additive genetic variance predicts permanent and continued response to selection (Bennett and Swiger, 1980). The study results therefore indicated that scab resistance is influenced majorly by the additive nature of inheritance.

Since any estimate of heritability is only relevant to a specific population in a specific set of environments (Wray and Visscher, 2008), a study by Afutu *et al.* (2016b), using another cowpea population, crossed 11 cowpea lines (parents) in a half diallel mating method. Results showed that Alegi, NE15 and NE48 had high negative general combining ability (GCA) effects and were therefore good parental lines for scab resistance improvement, while SECOW5T was the only parent with high positive GCA for improvement of both grain yield and 100 seed weight of cowpea. Additionally, for the number of seeds per pod, both the additive and non-additive gene effects were important, but for the number of pods per plant, it was the additive gene effects which was important. Other traits studied were controlled by the non-additive gene effects.

Limitations in developing resistance to stresses in cowpea. Implementation of research on the use of the advanced genomic resources of cowpea for the control of scab disease is still limited and this has hindered exploitation of this technique to improve cowpea production. The minicore population of 200 genotypes cowpea identified Single Nucleotide Polymorphism (SNP) markers Vigun08g220100, Vigun09g065900 and Vigun08g219500, to confer scab resistance to the minicore genotypes. This population could be a good source of scab disease resistance. However, further studies on the validation of these markers for improvement of scab resistance are still needed.

CONCLUSION

The review indicates the importance of evaluating the genetic basis of scab resistance as an aid to conventional breeding in the improvement of cowpea scab disease resistance. Utilizing more diverse cowpea populations will provide a wide genetic variability of the scab resistance trait leading to

increased response to selection and genetic gain (Acquaah, 2007). In addition, cowpea genotypes with high GCA will offer quantitative scab resistance, which will remain stable, durable and non-race specific to the different pathotypes of *Sphaceloma* scab, discovered in the different agro ecological zones.

It is also critical to use the advanced molecular and genomic approaches such as genomic prediction, Genome wide analysis studies, QTL mapping to increase the likelihood of selecting genotypes with high breeding value in order to speed up the development of Cowpea cultivars with stable and durable scab resistance.

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DECLARATION OF CONFLICT OF INTEREST

The authors have no conflict of interest to disclose.

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