African Journal of Rural Development, Vol. 10 (1):2025: pp. 55-70 ISSN 2415-2838

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Review of Cowpea Resistance to Flower Bud Thrips: Insights into Genetic, Secondary Metabolites and Environmental Interactions in Uganda

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ABSTRACT

Cowpea (*Vigna unguiculata* L. Walp) is an important legume crop in sub-Saharan Africa, valued for its high protein content and nutritional benefits. However, its production is severely hindered by biotic stresses, particularly flower bud thrips (*Megalurothrips sjostedti*), which cause significant yield losses by damaging flower buds and preventing pod formation. Although chemical pesticides are commonly used to control flower bud thrips, they pose environmental and health concerns, making alternative strategies critical. Host plant resistance, particularly through the exploitation of secondary metabolites, offers a promising, eco-friendly solution for managing flower bud thrips. This review highlights the biology of cowpea and flower bud thrips, examining the mechanisms of host plant resistance in cowpea, including morphological traits, plant defensive responses, and the role of secondary metabolites. It also explores the current progress in breeding for flower bud thrips resistance, emphasizing the need for genetic improvement using both conventional and molecular approaches, such as quantitative trait loci (QTL) mapping and genome-wide association studies (GWAS). Despite some success, the complexity of flower bud thrips resistance, environmental effects on metabolite production, and the inheritance patterns of secondary metabolites are not fully explored. The review concludes that further research into the biochemical and genetic basis of cowpea's resistance to flower bud thrips is crucial for developing more resistant varieties and ensuring sustainable cowpea production.

Keywords: Cowpea, flower bud thrips, host plant resistance, secondary metabolites

Cite as: Gitonga Wairimu, H., Kyamanywa, S., Edema, R., Hagos Abraha, R., Waniale, A. and Onziga Dramadri, I. 2025. Review of Cowpea Resistance to Flower Bud Thrips: Insights into Genetic, Secondary Metabolites and Environmental Interactions. *African Journal of Rural Development* 10 (1):55-70.

RÉSUMÉ

Le niébé (Vigna unguiculata (L. Walp)) est une légumineuse d’une importance majeure en Afrique subsaharienne, reconnue pour son apport élevé en protéines et ses bénéfices nutritionnels. Néanmoins, sa production subit de lourdes pertes dues aux stress biotiques, en particulier le thrips des boutons floraux (Megalurothrips sjostedti), qui provoque des dégâts notables en détériorant les boutons floraux et en freinant la formation des gousses. Bien que les pesticides chimiques soient fréquemment utilisés pour maîtriser ce ravageur, ils soulèvent des préoccupations environnementales et sanitaires, incitant à explorer des solutions alternatives. La résistance de la plante-hôte, particulièrement par l’exploitation de métabolites secondaires, offre une piste prometteuse et respectueuse de l’environnement pour combattre les thrips. Dans cet article, nous passons en revue la biologie du niébé et celle du thrips, en nous penchant sur les mécanismes de résistance inhérents, notamment les caractéristiques morphologiques, les défenses végétales et le rôle des métabolites secondaires. Les progrès actuels dans la sélection pour la résistance au thrips y sont examinés, avec un accent sur la nécessité d’approches génétiques, tant conventionnelles que moléculaires (cartographie QTL, GWAS). Malgré des résultats encourageants, la complexité de la résistance aux thrips, l’influence de l’environnement sur la production de métabolites et les modes d’héritabilité de ces composés ne sont pas totalement élucidés. La conclusion insiste sur l’importance d’une recherche approfondie des mécanismes biochimiques et génétiques de la résistance du niébé au thrips des boutons floraux, étape cruciale pour concevoir des variétés plus résistantes et assurer la pérennité de la production de niébé.

Mots-clés : niébé, thrips des boutons floraux, résistance de la plante-hôte, métabolites secondaires

INTRODUCTION

Cowpea (*Vigna unguiculata* L. Walp.) is a multipurpose legume crop, particularly in Africa, where it serves as a key source of plant protein for human and livestock consumption (Singh, 2006). Its adaptability to varying environments and ability to provide nutritional and economic benefits make it an essential component of agricultural systems (Aliyu and Makinde, 2016). Despite its significance, cowpea production faces considerable challenges from biotic and abiotic stresses, among which pests, particularly flower bud thrips (*Megalurothrips sjostedti*), are a major concern. Flower bud thrips damage cowpea plants at the flowering stage, resulting in significant yield losses, which can range from 20% to 80% (Karungi *et al*., 2000). These losses pose a threat to food security and economic stability, especially in regions heavily reliant on cowpea cultivation.

Traditionally, the management of flower bud thrips has relied heavily on synthetic pesticides (Kyamanywa, 1996; Karungi *et al.,* 2000). Although effective, this method raises environmental and health concerns, including the development of pestcide resistance, pollution, and the accumulation of toxic residues in food (Abtew *et al.,* 2015a). In response to these challenges, researchers are exploring host plant resistance as a sustainable and environmentally friendly alternative for flower bud thrips management. This approach leverages cowpea's inherent genetic resistance mechanisms, including structural traits, biochemical pathways, and secondary metabolite production, to deter flower bud thrips infestation and minimize damage (Adati *et al.,* 2008; Togola *et al.,* 2019). However, limited sources of flower bud thrips resistant cowpea varieties, inadequate application of molecular markers in breeding programs, and insufficient understanding of how environmental factors influence secondary metabolite production hinder progress towards breeding for resistance. Furthermore, the genetic basis and inheritance of plant secondary metabolites are not well understood, complicating efforts to develop resilient cowpea varieties.

This review aims to examine existing research on cowpea resistance to flower bud thrips, highlighting advances in host plant resistance mechanisms, the role of secondary metabolites, how they are influenced by environmental factors and the inheritance of secondary metabolites associated with resistance of cowpea to flower bud thrips. By addressing these gaps, the study contributes to the development of sustainable strategies for enhancing cowpea productivity and resilience, thus supporting food security and economic livelihoods of the small holder farmers.

Origin and Biology of Cowpea

Cowpea (*Vigna unguiculata* L. Walp.) also known as black eye pea is an annual legume belonging to the family Fabaceae. The history of cowpea dates to ancient West African cereal farming, about 6000 years ago, where it was closely associated with the cultivation of sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) (Davis *et al.*, 1996). The crop originated in Africa and is currently widely grown in Africa, Latin America, Southeast Asia and in the southern United States (Boukar *et al.*, 2015).

Vigna unguiculata is known for its diverse growth habit (Davis *et al.*, 1996). It can be erect, determinate, indeterminate, non-branching, and climbing with profuse branching. The crop has robust tap root system with numerous lateral roots. The stems are cylindrical and a little ribbed, twisting, occasionally hollow and glabrous. Stems may be green or pigmented. The leaves are alternate, trifoliate, with one symmetrical terminal leaflet and two asymmetrical leaflets. Petioles are 3-25 cm long with a swollen pulvinus at the base. The flowers are borne in multiple racemes. Flower stalks (peduncles) arise from the leaf axil. Inflorescence is a non-branched axillary raceme bearing several flowers at the terminal end of peduncles which vary from 5 to 60 cm in length and are slightly twisted and ribbed. Calyx is longitudinally ribbed, tubular with 2-15 mm long sub-equal lobes. The corolla is papilionaceous with an erect standard petal spreading at anthesis. The pigmentation arrangement of corolla differs from white to solid violet with yellow spots near the base of the standard petal. The stamens are diadelphous (9+1) and the anthers are bright yellow. The ovary is monocarpellary, unilocular with many ovules. Pods are overhanging or vertically attached to the raceme axis and they are mostly lined, although curved and coiled shapes are also common (Boukar *et al.*, 2015).

Cowpea pod length may vary from less than 11 to more than 30cm (Davis *et al.*, 1996). The pods are smooth, long, cylindrical and slightly curved. As the seeds approach the green-mature stage for use as a vegetable, pod color may be distinctive, most commonly green, yellow or purple. As the seeds dry, the pod color of the green and yellow types becomes tan or brown (Boukar *et al.*, 2015). Two or three pods per peduncle are common but often four or more pods are carried on a single peduncle. The presence of these long peduncles is a distinguishing feature for cowpea and this characteristic also facilitates harvest. Cowpea primarily is self-pollinating (Huynh *et al.*, 2013).

The number of seeds per pod vary. Seed shape is a major characteristic correlated with seed development in the pod. Seeds develop a kidney shape if not restricted within the pod. When seed growth is restricted by the pod, they become progressively more globular. The seed coat is either smooth or wrinkled and of different colors including white, cream, green, red, brown, and black. Seed may also be speckled, mottled, or blotchy (Davis *et al.*, 1996).

V. unguiculata has 2n = 2x = 22 chromosomes and an estimated genome size of 613 mb. It is reported that the 11 bivalent complement, consists of 1 short (19 µm), 7 medium (26-36µm), and 3 long (41-45 µm) chromosomes (Huynh *et al.*, 2013). The chromosomes are small and difficult to manipulate (Davis *et al.*, 1996).

Importance of cowpea

Cowpea is valued for its nutritious qualities found in grain, leaves and haulms which are consumed by human and livestock. The haulms are also used as beddings or green manure in the farm. The grain is rich in protein (30%) and iron while the leaves too have a considerable amount of proteins (Singh, 2006). The protein in cowpea seed has high number of amino acids, lysine and tryptophan, compared to cereal grains, which are important in proper functioning of the body. Cowpea can be used at all stages of growth. The tender green leaves are an important food sauce in Africa and are prepared as a pot herb, like spinach. Immature pods are used in the same way as French beans (*Phaseolus vulgaris*), often being mixed with other foods. Green cowpea seeds are boiled as a fresh vegetable, or may be canned or frozen. Dry mature seeds are also suitable for boiling and canning (Sabiti *et al*., 1994). Being drought tolerant, the crop is significant in attaining food security in Uganda considering the rapid climate change. In addition, farmers get income from the crop by selling the grain and/or the leaves (Aliyu and Makinde, 2016).

Cowpea production. Globally, over 12 million ha of land is under cowpea production yielding approximately 6.9 million tonnes of grain annually (FAOSTAT, 2020). About 83% of world cowpea production is in Africa, with approximately 80% of this being in West Africa. The leading cowpea producers in the world are Nigeria, Niger, Brazil and Burkina Faso with approximately 45%, 15%, 12% and 5% of the world production respectively (FAOSTAT, 2020). In Uganda, Cowpea is the fourth most important legume food crop after the common beans (*Phaseolus vulgaris* L.), soya bean (*Glycine max*) and groundnuts (*Arachis hypogea* L.) (Fatokun *et al.,* 2012). The production is mostly in the Eastern and Northern regions with estimated 2.2 million Small holder farmers growing the crop using simple traditional methods. In Uganda, cowpea production has been stagnant over the past few years compared to the world production (FAOSTAT 2023) (Figure 1), possibly due to production contraints, both biotic and abiotic.

Constraints to cowpea production

Despite its importance and the wide adaptation in sub-Saharan Africa (SSA), cowpea is threatened by biotic and abiotic stresses (Duche *et al.,* 2015). The abiotic factors affecting cowpea production include soil, drought and heat. Biotic factors important in cowpea production are pests and diseases. Several pests, including flower bud thrips (*Megalurothrips Sjostedti*) cause yield reduction in cowpea production (Singh, 2006). Flower bud thrips cause about 20-80% yield reduction in Cowpea (Karungi *et al.,* 2000). It is the first pest appearing on the cowpea plant at reproductive stage (Taylor, 1969). The pest attacks the crop at flowering stage leading to destruction and failure of bud formation. Other pests that are of economic importance to cowpea production include pod borer (*Maruca vitrata*), Aphids (*Aphis craccivora*) and pod sucking bugs (*Clavigralla tomentosicollis*). In addition, diseases such as scab (*Sphaceloma* sp.), bacterial blight (*Xanthomonas axonopodis*), *Cercospora* leaf spot and viruses also contribute to cowpea's low production (Adipala *et al.,* 2001).

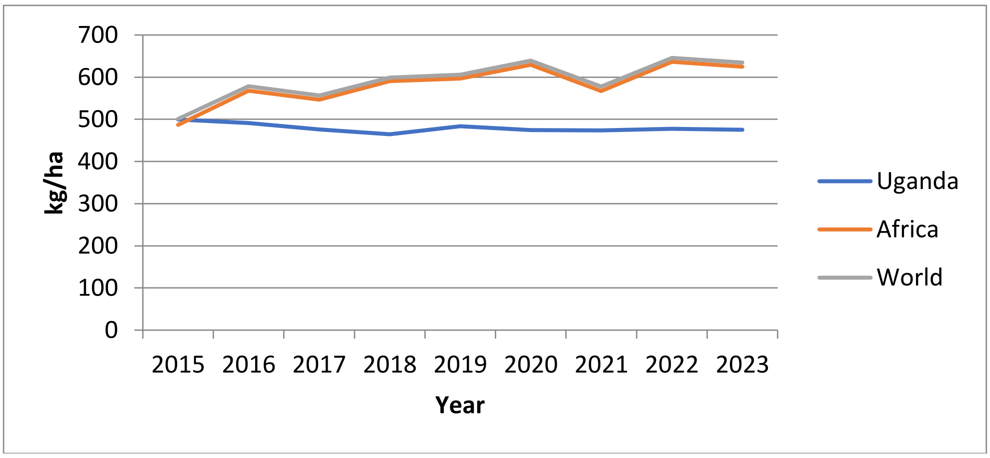

Figure 1. Production (kg/ha) of cowpea in Uganda, Africa and world in the past ten years.

Biology of flower bud thrips and damage on cowpea. The cowpea flower bud thrips also known as African bean flower thrips are shiny, black, slender, small-winged insects that feed on flower buds and flowers (Figure 2A). It is classified in the family Thripidae in order Thysanoptera. The insect's life cycle takes 14-18 days. Eggs are laid in flower buds and nymphs feed on the plant, causing extensive damage. Pupae develop in the soil (Ekesi *et al*., 1998). During the pre-flowering period, nymphs and adults may damage the terminal buds. However, the main damage is on the flower buds and flowers. Flower bud thrips extract sap from vascular elements by means of stylets. Damaged flowers are distorted and malformed. They change colour and may fall off early, with the result that pods are not formed (Figure 2B). If pods begin to form and become infested, they will be malformed (Oparaeke *et al*., 2008). Flower bud thrips are found throughout Sub-sahara Africa (SSA), both in regions with heavy rainfall and semi-arid regions. Infestation can occur when adults fly from other host plants such as weeds infest cowpea plants (Ekesi *et al*., 1998).

Management of flower bud thrips in cowpea. Synthetic pesticide is the most commonly adapted method for flower bud thrips control with at least 2 sprays at bud formation and flowering. It was recommended that the first spray be done when there are 22 flower bud thrips per 25 cowpea flowers while the second spray should be done when there are 90 flower bud thrips per 25 cowpea flowers (Bal, 1991). Synthetic pesticides have been successfully used in control of cowpea pests with increased yield being reported in Nigeria (Alghali, 1992), Kenya (Kyamanywa, 1996), Cameroon and Uganda (Karungi *et al*., 2000). However, due to the environmental pollution caused by synthetic pesticide (Branchet *et al*., 2018), the risk of pest resistance to pesticide, accumulation of toxic residues in food,pose health risks to consumers and livestock (Egho *et al*., 2011). Hense, researchers innovated organic ways of managing flower bud thrips. Bio-pesticides extracted from the leaves of *Annona senegalensis*, *Lippia rugosa* and *Jatropha curcas* were reported to control flower bud thrips in cowpea in Cameroon (Vandi *et al*., 2020). It was however reported that climate, wind, nutrition, and mode of application of the bio-pesticide influence their efficacy in controlling flower bud thrips (Solsoloy *et al*., 1997; Bambara *et al*., 2008). Other methods applied in control of flower bud thrips include use of microsymbionts, rhizobia and arbuscular mycorrhiza fungi (AMF), and the mycopesticide *Metarhizium anisopliae* which contributed to significant reduction in flower bud thrips population and increased number of flowers (Ekesi *et al*., 1998). These biofertilizer and biopesticide do not cause direct injury to the pest but rather causes physiological changes in the plant which interfere with flower bud thrips feeding (Ngakou *et al*., 2008). A challenge to this method is that high volume spray is necessary for effective control (Ngakou *et al*., 2008). Plant-based extract has also been used as repellant against flower bud thrips. The extracts contain different secondary metabolites that act as feeding deterrent, repellents and toxins, which play a role in defense against pests (Maia *et al*., 2015). *Piper nigrum*, *Cinnamomum zeylanicum* and *Cinnamomum cassia* were reported to contain secondary metabolites which repelled flower bud thrips in cowpea (Abtew *et al*., 2015b). Other methods that have been suggested to famers for control of flower bud thrips are proper land preparation, and early planting among others. In addition, use of cowpea varieties resistant to flower bud thrips has been highly encouraged (Abudulai *et al*., 2006; Togola *et al*., 2019; Karungi *et al*., 2000).

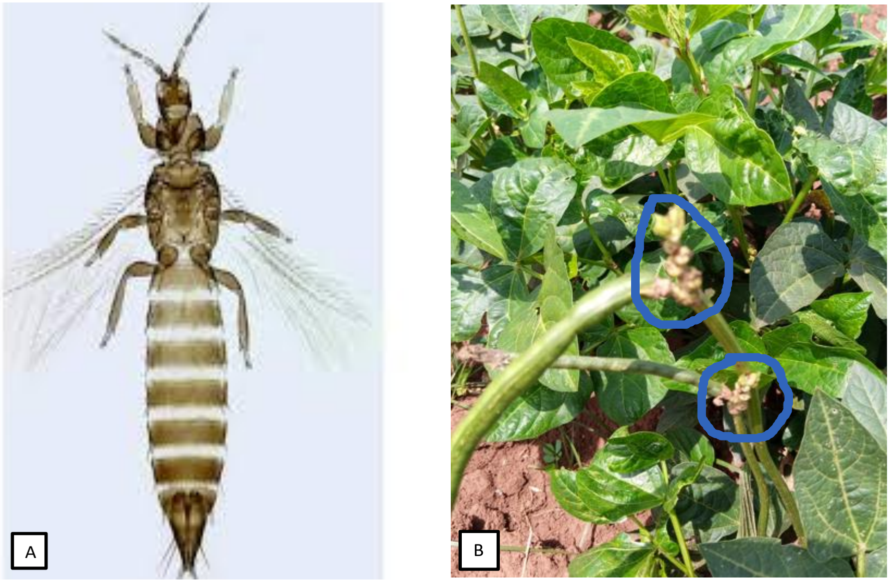

Figure 2. A. Flower bud thrips. B. Flower abscission caused by flower bud thrips damage hence no pod formation.

Mechanism of cowpea resistance to flower bud thrips. Cowpea host plant resistance is significant for long-term management of flower bud thrips. The concept of host plant resistance aims at integrating preventive and curative measures where the host plant plays the biggest role (Mouden and Leiss, 2021). Host plant resistance is a complex mechanism ranging from morphological barrier to signaling molecules of the immune system in the plant (Kaur *et al.*, 2018). Pubescence and trichomes are examples of morphological structures contributing to resistance of plants to pests (Kaur *et al.*, 2018). Plant defensive responses can be pre-existing or induced upon attack by the pest. Subsequently, the genetic make-up of the cowpea genotype determines resistance or susceptibility to flower bud thrips (Alabi, 2014; Oladejo *et al.*, 2017. On the other hand, induced resistance has been found to be important whereby upon attack by flower bud thrips, the plant hormone jasmonic acid leads in signaling the plant to respond by production of deterrent factors such as secondary metabolites and volatile organic compounds (Shrivastava *et al.*, 2010; Diabate *et al.*, 2019; Ren *et al.*, 2020.

Induced resistance depends on plant receptors. The plant recognizes the herbivore-associated elicitors (HAEs), herbivore effectors or herbivore associated molecular patterns (HAMPs) (Bonaventure *et al.*, 2011). The recognition activates signal transduction pathways that link herbivore-specific elicitors to the expression of suitable defense genes (Santamaria *et al.*, 2013). Once the plant perceives the presence of pest, the damaged tissues induce mitogen activated proteins kinase, jasmonic acid and/or ethylene biosynthesis as defense response. In addition, elicitors may be released by cell death as fragment molecules and reactive oxygen species (ROS), which are recognized as alarm signals (Gilardoni *et al.*, 2011). These reactions triggers response in plants hence host plant resistance.

Field evaluation of cowpea for resistant to flower thrips. Efforts have been made to identify resistant genotypes to lessen the damage caused by flower bud thrips through screening of germplasm available in different countries. Extensive research on cowpea has been done at International Institute of Tropical Agriculture (IITA) in Nigeria which is maintaining about 15,000 cultivated cowpea accessions and more than 2,000 wild relatives. Mining these resources has resulted in identification of several sources of resistance to flower bud thrips (Alabi *et al.*, 2010; Oladejo *et al.*, 2017). Consequently, intensive efforts have been made to develop varieties of cowpea that are resistant to flower bud thrips in Africa using both conventional and modern molecular approaches (Omo-ikerodah *et al.*, 2009; Boukar *et al.*, 2016; Agbahoungba *et al.*, 2017 ; Sobda *et al.*, 2017;

Mbeyagala *et al.*, 2018; Togola *et al.*, 2019). Accordingly, cowpea genotypes have been found to respond to flower bud thrips differently in various environments. Phenotyping of cowpea for flower bud thrips resistance has been done in field under natural infestation and in screen house with artificial inoculation (Omo-ikerodah *et al.*, 2009; Agbahoungba *et al.*, 2017. In Uganda, Agbahoungba *et al.*, (2017) screened cowpea genotypes from IITA and landraces for resistance to flower bud thrips in three locations and two seasons. Among the 70 genotypes that were tested, IT2841*Brown, MU20B, EBELAT*NE39 were found to be most resistant to flower bud thrips across the three locations. This is an indication of the few resistant genotypes among populations, hence the need to identify more sources of resistence.

In order to identify some valuable resistant genes, it is necessary to screen a diverse population of cowpea. A cowpea minicore population was developed by the University of California Riverside. It is composed of 368 accessions from 50 countries including 242 landraces, 98 breeding lines, 3 genotypes categorized as “weedy,” and 25 genotypes that are not categorized. The population was a selection from 5,000 genotypes based on their geographical zone. Genetic and phenotypic assessments of diverse collections are required to utilize their potential in breeding programs (Muñoz-Amatriaín *et al.*, 2021). Although the population was used to identify sources of resistance to flower thrips in Nigeria (Togola *et al.*, 2019), it has not been evaluated for resistance to thrips in Uganda. Being a diverse population, it has potential to habour resistant genes which could be introgressed into locally adapted genotypes susceptible to flower bud thrips.

Molecular studies of cowpea resistance to flower bud thrips. Various quantitative trait loci (QTL) for flower bud thrips resistance in cowpea have been identified in recent studies. Omo-ikerodah *et al.* (2009) used a cowpea linkage map of amplified fragment length polymorphism (AFLP) markers to identify QTLs for resistance to flower bud thrips using recombinant inbred lines (RILs) derived from a cross between ‘Sanzi’ (resistant) and ‘VITA7’ (susceptible) genotypes in Nigeria. Five QTLs were identified and arranged according to their contributions to resistance of flower bud thrips in descending order as follows: LG3, LG2, LG6, LG7, and LG1. The QTLs were designated *FTh1*, *FTh2*, *FTh3*, *FTh4*, and *FTh5* respectively. The phenotypic variance explained by the QTLs were 32.0, 18.4, 12.6, 11.9 and 9.5%, respectively. Sobda *et al.* (2017), using SNP markers detected three QTLs for flower bud thrips in cowpea in Cameroon, using F_2 of a cross between resistant parent Sanzi and susceptible parent VYA. The QTLs detected were referred to as *Fthp28*, *Fthp87* and *Fthp12* on chromosome 2, 4 and 6, respectively. In their effort to identify QTLs for resistance to flower bud thrips in cowpea, Agbahoungba *et al.* (2018a) detected markers for Cowpea flower bud thrips resistance in Uganda using simple sequence repeats (SSR). The study identified markers CP37/38 and CP215/216 that were significantly associated with flower bud thrips damage scores and flower bud thrips counts respectively. These markers explained 7 and 11.2% of the total phenotypic variance in flower bud thrips damage scores and flower bud thrips counts respectively, indicating that the markers identified are still far from the genes controlling the resistance to flower bud thrips. The marker effects observed were low as compared to 77.5 and 43.2% observed by Omo-ikerodah *et al.*, (2009) and Sobda *et al.* (2017) in Nigeria and Cameroon, respectively. This indicate that the resistance of cowpea to flower bud thrips is probably controlled by several genes and the identified markers were not able to cover most of these genes. It is therefore necessary to identify more markers using different approach.

Genome Wide Association Study (GWAS) is an alternative method for detecting QTLs and has been used widely in QTL mapping for important economic traits such as yield and its components (Mei *et al.*, 2013; Qin *et al.*, 2015), and resistance traits (Zhao *et al.*, 2014). In GWAS, a collection of diverse lines that have been genotyped and phenotyped for traits of interest are used to identify genomic loci linked to quantitative traits (Varshney *et al.*, 2014). In comparison to quantitative trait loci studies which are achieved using pedigrees (e.g., bi-parental crosses), GWAS has the advantage of detecting smaller chromosomal regions affecting a trait hence provide precise estimates of the size and direction of the effects of alleles in known loci (Aboul-maaty and Oraby, 2019). In recent years GWAS has become a more cost-effective tool for detecting important QTLs or genes associated with complex traits compared to linkage mapping. It is an effective tool to separate the genetic architecture of complex traits in cowpea and other crops (Lucas *et al.,* 2011). Association mapping for different traits in a number of crop species such as rice (*Oryza sativa*), corn (*Zea mays*), soybean (*Glycine max*), wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), tomato (*Solanum lycopersicum*) and potato (*Solanum tuberlosum*) have been conducted (Mei *et al*., 2013; Zhao *et al*., 2014; Qin *et al*., 2015). Association mapping studies were also conducted for seed size and pod length in Cowpea (Lo *et al*., 2018; Xu *et al*., 2017). In Uganda, Miesho *et al*. (2019) used genome wide association to study the resistance of bruchid (*Callosobruchus maculatus*) in cowpea minicore population. Although extensive molecular studies have been done on cowpea resistance to flower bud thrips, few have used GWAS technology. Moreover, the technology has not been used in study of flower bud thrips in cowpea breeding program in Uganda. With the recent completion of cowpea genome sequencing, rapid identification of genes for cowpea resistance to flower thrips using GWAS is possible. High-resolution genetic maps provide powerful tools for identifying and analyzing genes of interest (Liang *et al*., 2015). At the University of California, 51,128 SNPs have been developed for the cowpea genome using the “Cowpea iSelect Consortium Array” using minicore population (Lonardi *et al*., 2019). However, they have not been used for genome wide association study of cowpea resistance to flower bud thrips which limit use of marker assisted selection in development of cowpea resistant to flower bud thrips.

Role of Secondary metabolites in plant defense. Plants produce diverse array of organic compounds. The organic compounds that are directly involved in plant development such as photosynthesis, transpiration and reproduction are known as primary metabolites while those not directly involved for instance phenolics are known as secondary metabolites (Erb and Reymond, 2019). Secondary metabolites are important in plant defense against herbivores through reduction of nutritive value of plant food or as feeding deterrents or toxins (Belete, 2018). The metabolites do not affect the normal growth of the plant but reduce the palatability of the plant to the herbivore. They do not only defend the plant but also improve the fitness of the plant in different environments (Belete, 2018).

Some of the secondary metabolites that have been found to play role in plant defense are phenolics, lignin, tannins, proteins, antioxidants, lectins, lignin and flavonoids (Bennett *et al*., 2011). Plant phenols are the largest group of plant defense secondary metabolites which play the major role in host plant resistance (Singha *et al*., 2011). Apart from herbivory, phenolics also act as defense from competing plants and microorganisms. Flavonoids are toxic to cells and play a defensive role through complexation. In addition, they influence the behavior, growth and development of the insect (Bennett *et al*., 2011). Upon exposure to stress conditions, the flavonoid biosynthetic genes are induced, thereby increasing the flavonoid levels, particularly during wounding. The stress results in the production and accumulation of reactive oxygen species (ROS), which damage the cell components (Baskar *et al*., 2018). To combat these conditions, plants produce flavonoids which are involved in the suppression of generation of ROS, as well as reducing the ROS once formed. In order to regulate the production of flavonoid and other secondary metabolites, plants use controlled mechanism of gene expression mediated by transcription factors. The transcription factors help to switch on and off the activities against flower bud thrips.

Some of the transcription factors that regulate flavonoids pathway gene are WD40 and MYB (Hichri *et al*., 2011). WD40 repeat proteins are very abundant protein family which provides a rigid network for the interaction of proteins with other cellular components. It controls the signal cascades, cellular transport and apoptosis in influencing transcription (Dressel and Hemleben, 2009). Similarly, antioxidants play a role in the detoxification of ROS induced during abiotic and biotic stresses in plants. Plant flavonoids and other phenolic compounds are stored in specialized tissues and are dislocated to the racemes/flower when flower bud thrips infestation occurs. In the infected plants, secondary metabolites accumulate at the site of infection in order to induce the hypersensitivity reaction and programmed cell death. The pest invasion is blocked by the formation of callus and tylose (Beckman, 2000). On the other hand, lignin increases the toughness of the plant tissue thereby limiting feeding by insect. It also reduces the nutrients of the plant near the epidermal layer and physically blocks insects from feeding or entry (Belete, 2018). When the plant is attacked by insect, lignin synthesis increases thereby reducing insect fecundity. Insect attack and other stresses lead to changes in quantity and quality of proteins, which in turn affects signal transduction and oxidative defense (Erb and Reymond, 2019). Some proteins are not harmful to insects and will remain stable in the gut while some are toxic (Haughn *et al.,* 1991). Protease is the enzyme responsible for the toxicity observed in plants against insects. Tannins on the other hand bind to proteins thereby reducing the nutrient absorption efficiency and cause midgut lesions thereby affecting the development of the insect. They are bitter and deterrent to a wide range of insects. When insects ingest plant parts containing tannins, the digestibility is reduced hence decreased nutritive value of plant parts to insect (Erb and Reymond, 2019).

Environment-metabolites interaction effect on host plant resistance. Since plants are immobile, they adopt resistance mechanisms that enable them survive adverse environments and retain their fitness. On the other hand, insects dependent on living plant cells to complete their life cycles. Many pests are tissue- or cell-specific. Flower bud thrips feed mainly on cowpea racemes, flower and flower buds hence interfering with metabolism of the plant in these parts. Plants respond to pest attack through production of secondary metabolites as immune response. Synthesis and accumulation of plant secondary metabolites critically depend on environmental conditions where the crop is grown (Erb and Reymond, 2019). Soil factors, temperature, light and soil water/rainfall, may significantly affect plant processes that are important in growth and development and their ability to produce secondary metabolites (Shohael *et al.,* 2006). In other words, plant secondary metabolites synthesis is influenced by environmental changes which may positively or negatively affect the survival of the plant (Belete, 2018). For example, the biosynthesis of secondary metabolites is associated with high temperature in plants (Verma and Shukla, 2015). High-temperature stress usually increases the production of secondary metabolites, whereas some studies indicate that secondary metabolites were decreased in plants under high-temperature (Li *et al.,* 2020). Therefore, the increase or decrease of secondary metabolites in response to elevated temperatures is dependent on the species and multiple factors (Verma and Shukla, 2015).

Effect of environment in production of plant secondary metabolites. Plant metabolites have been found to have some toxic effect to pests (Saxena, 1985). The role of secondary metabolites in defense may involve deterrence/antifeedant activity, toxicity or acting as precursors to physical defense systems. The production of some of the plant secondary metabolites is induced as a result of infection or wounding. The speed at which these metabolites are produced after induction is determined by the genetic makeup of the plant, temperature and rainfall conditions in which the crop is growing (Erb and Reymond, 2019).

Studies have shown that some primary and secondary metabolites in plant cause the crop to resist pests (Mazid *et al*., 2011; Mwila *et al*., 2017). In cowpea, secondary metabolites have been found to play a role in resistance to flower bud thrips (Alabi *et al*., 2011; Agbahoungba *et al*. 2018b). Agbahoungba *et al*. (2018b) studied the role of metabolites of cowpea’s reproductive structures in respect to resistance to flower bud thrips damage in Uganda. They found out that flavonoids, total reducing sugars and total carbon conferred resistance to flower bud thrips when in large amounts in the stipules, floral buds and flowers, while soluble amino acid resulted to susceptibility. The study used genotypes IT2841*Brown, TVU1509, Sanzi (Resistant) and NE4, WC52, WC36 (Susceptible). In a similar study, high levels of total proteins increased susceptibility to flower bud thrips (Alabi *et al.,* 2011), which is associated with preference for feeding and reproduction by the pest (Olatunde and Odebiyi, 1991). These studies however did not look at how these metabolites respond to different environments, which might influence resistance.

Environmental conditions such as temperature and moisture conditions affect the biochemical and physiological plant defensive mechanisms leading to alteration in metabolite pathways of affected plants, sometimes causing a negative impact on plant insect interactions and plant fitness (Ncube *et al*., 2012; Kant *et al*., 2015; Jamieson *et al.*, 2017). Some studies have reported the complexity of plant responses to combinations of attacks making it impossible to directly infer from pairwise plant-insect interactions (Barah and Bones, 2015). Depending on the different pathways, biotic changes can trigger many metabolites products such as antioxidants, proteins and phenolics (War *et al.*, 2012; Fürstenberg-hägg *et al.*, 2013). During growth of the plant, the environmental signals in their pathways lead to different response of the plants as a way of adapting to the changing environment (Fürstenberg-hägg *et al.*, 2013). These changes however, do not occur in a predictive manner (Moore *et al.*, 2014). Information on plasticity of secondary metabolites associated with resistance of cowpea to flower bud thrips and their interaction in four varying environment was reported in Uganda (Gitonga *et al.*, 2022). The study used secondary metabolites phenolics, flavonoids, antioxidants, reducing sugars, proteins, lignin and tannins to investigate their response to different environments in presence of flower bud thrips. The study reported fluctuating levels of secondary metabolites in different environments with flavonoid, being more stable across environments. The stability of the metabolites however, was depended on the cowpea genotype, hence the need to conduct experiments using different genotypes in the breeding pipeline. The information is necessary for recommending genotypes for specific environments.

Inheritance of resistance of cowpea to flower bud thrips and secondary metabolites. Inheritance of different plant secondary metabolites has been studied in trees and crops. In white birch tree, the inheritance of volatile secondary metabolites was conditioned by dominant gene and maternal effects (Isidorov *et al.*, 2019). Elsewhere, in Eucalyptus, non-dominance effect was reported to be major mode of inheritance of secondary metabolites, among the tannins and phenolics (O'Reilly-Wapstra *et al.*, 2014). Inheritance of total isofavonoid content in soya bean was found to be controlled by additive gene effect (Bi *et al.*, 2015). On the other hand, in tomato (*Solanum lycopersicum*), inheritance of different secondary metabolites was controlled by dominant gene effect (Alseekh *et al.*, 2015), additive, non-additive and reciprocal effects (Bineau *et al.*, 2022). Also, overdominance and dominance mode of gene action was observed for flavonoids in foxtail millet (*Setaria italica*) (Li *et al.*, 2018). The model plant, *Arabidopsis thaliana*'s inheritance of secondary metabolites was due to non-additive/epistasis effects (Cubillos *et al.*, 2018). In cowpea, inheritance of secondary metabolites responsible for resistance to flower bud thrips was studied on five genotypes crossed in full diallel method (Gitonga *et al.*, 2023). The findings indicated Flavonoids, antioxidants, proteins and reducing sugars as predominantly being controlled by additive and dominance gene effects, an indication that these traits are heritable and can be used as selection tools for resistance to flower bud thrips. Inheritance is specific to germplasm being tested and the testing environments (Umar *et al.*, 2014), hence the need to conduct such studies on different available germplasm.

CONCLUSION

Cowpea is a vital legume crop but its production is significantly hindered by flower bud thrips, leading to substantial yield losses. While chemical control methods have been widely used, concerns over environmental and health impacts necessitate use of alternative solutions. Host plant resistance presents a sustainable and environmental friendly approach to managing this pest. This review highlighted the complexity of cowpea resistance to flower bud thrips, emphasizing the roles of biochemical responses and genetic mechanisms. Although some progress has been made in breeding for resistance, challenges remain, including the limited availability of resistant genotypes, insufficient application of molecular markers, and the influence of environmental factors on secondary metabolite production. Future research should focus on identifying more resistant cowpea genotypes, enhancing marker-assisted selection, and exploring plant-environment interactions to improve breeding efficiency. A deeper understanding of the biochemical and genetic basis of resistance will be crucial for developing cow pea varieties with durable resistance, ensuring sustainable cowpea production, and supporting food security in Uganda and other regions reliant on this important crop.

ACKNOWLEDGEMENT This paper is an output of the first Author's Post- Doctorial fellowship at Makerere University Regional Centre for Crop Improvement (MaRCCI) funded by the Regional Universities Forum for Capacity Building in Agriculture (RUFORUM) with funding from Carnegie Corporation of New York Grant.

STATEMENT OF NO-CONFLICT OF INTEREST

The Authors declare no conflict of interest in the paper.

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