INHERITANCE OF RESISTANCE TO FLOWER BUD THRIPS (*MEGALUROTHRIPS SJOSTEDTI*) IN COWPEA

A THESIS SUBMITTED TO THE SCHOOL OF GRADUATE STUDIES, KWAME NKRUMAH UNIVERSITY OF SCIENCE AND TECHNOLOGY, IN PARTIAL FULFILMENT OF THE REQUIREMENT FOR THE DEGREE OF MASTER OF SCIENCE IN AGRONOMY (PLANT BREEDING)

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AUGUST, 2012

DECLARATION

I hereby declare that, I have under supervision undertaken the study and except for specific references which have been duly and appropriately acknowledged, this project is the result of my own research and has not been submitted either in part or whole for other degree elsewhere.

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We declare that we have supervised the student in undertaking the study submitted herein and confirm that he has our permission to submit.

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Prof. Richard Akromah

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DEDICATION

This thesis is dedicated to Prof. R.C. Abaidoo and Prof. Richard Akromah for being the inspirational force behind my studies

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ABSTRACT

Flower bud thrips is a major pest of cowpea that causes significant grain yield losses. Chemical control measures are the most widely known form of control to this pest. However, the rapid development of insecticide resistance in thrips population has rendered the chemical treatments ineffective. The development of flower bud thrips resistant varieties is necessary to help curb the situation. Knowledge of inheritance of flower bud thrips resistance is required to accelerate breeding of resistant varieties. Inheritance of resistance to flower bud thrips in cowpea was studied in a cross involving resistant (Sanzi) and susceptible (Bengpla) genotypes, using generation mean analysis. The segregating generations were intermediate between the resistant and susceptible parents and were skewed towards the resistant parent. Reciprocal differences were not detected in the cross suggesting the absence of maternal effect. The results revealed a non-significant departure from zero for parameters A, B and C and a non-significant chi-square (χ^2) for joint scaling test indicating adequacy of the additive-dominance model in explaining the mode of inheritance of resistance to flower bud thrips in cowpea. The additive-dominance model revealed that both additive and dominance gene effects contributed significantly to the inheritance of resistance to flower bud thrips suggesting the potential for further improvement of the trait using simple selection and hybridization procedures. Dominance gene effect was negative indicating dominance in the direction of the resistant parent. Negative heterosis over mid-parent was observed for thrips resistance score. Estimates of broad sense and narrow sense heritabilities indicated that environmental effects were larger than genetic effects. The results suggested the imposition of lower selection pressure in order to advance as many high-potential recombinants as possible in a hybridization programme.

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CHAPTER 1

1.0 INTRODUCTION

1.1 BACKGROUND INFORMATION

The most well-known Papilionaceae species with an African origin is *Vigna unguiculata* (L) walp (cowpea) (Schippers, 2002). Cowpea is grown worldwide with an estimated cultivation area of about 14.5 million hectares annually and an annual worldwide production of over 4.5 million metric tons (Singh *et al*., 2002). Subsistence farmers in countries such as Nigeria, Niger, Mali and Malawi in Africa and Myanmar in South East Asia are the main producers of cowpea (Fowler, 2000). Cowpea exhibits different morphological forms; some are prostrate, erect or climbing. The leaves are trifoliate; inflorescences are axillary with few crowded flowers near the tip in alternate pairs. The anthers bear sticky and heavy pollen grains (Purseglove, 1984).

Cowpea is produced for household purposes and as a cash crop. It is a multipurpose crop, since it is cultivated for leaf and seed yield (Schippers, 2002). It is a multifunctional crop, providing food for man and livestock and serving as a valuable and dependable revenue-generating commodity for farmers and grain traders (Singh, 2002; Langyintuo *et al*., 2003). Cowpea contributes 30-125 Kg N/ha in the soil due to its nitrogen fixing properties (Ennin-Kwabiah and Osei-Bonsu, 1993) and also serves as a residue, which benefits the succeeding crops. It is also a shade tolerant crop and, therefore, compatible as an intercrop with a number of cereals and root crops, as well as with cotton, sugarcane and several plantation crops. Coupled with these attributes, its quick growth and rapid ground cover have made cowpea an essential component of sustainable subsistence agriculture in

marginal lands and drier regions of the tropics, where rainfall is scanty and soils are sandy with little organic matter (Singh *et al*., 1997).

Cowpea is the main food legume in tropical Africa (Padulosi and Ng, 1997) and is a very important source of protein as well as carbohydrate in the diets of relatively poor people in developing countries (Elias *et al.,* 1964). In fresh form, the young leaves and immature pods are used as vegetables, while the grain is used in the preparation of several dishes. According to Bressani (1985), the mature legume contains 23-25% protein and 50-67% carbohydrate, 1.9% fats, 6.35% fibre and small percentage of the B-vitamins such as folic acid, thiamine, riboflavin and niacin as well as some micronutrients such as iron and zinc. The relative composition of carbohydrates and their richness in protein make them important components of the food ration of humans particularly where there is insufficiency of proteins of animal origin, a typical situation in many tropical developing countries (Singh and Rachie, 1985). The foliage and stems are also good source of fodder for livestock as well as a green manure and a cover crop.

1.2 PROBLEM STATEMENT

Cowpea faces numerous production constraints despite its importance. Insect pests, plant diseases, parasitic flowering plants and drought are major yield-reducing factors (Terao *et al.*, 1997). The low yields become more striking when it is realized that the average yield of cowpea in West and Central Africa is about 0.24 t/ha (Quin, 1997) in spite of the fact that there are a number of cowpea lines that with proper management, can yield above 2.0 t/ha (Duke, 1990; Singh *et al.,* 1997). Several insect pests attack the crop in the field and at

storage, with the flower bud thrips (*Megalurothrips sjostedti*) being one of the most damaging in Africa (Jackai and Daoust, 1986; Jackai *et al*., 1992).

Flower bud thrips is a major pest of cowpea that causes considerable grain yield losses. In West Africa, the flower bud thrips, *M. sjostedti* is the most economically important thrips pest of cowpea causing yield losses between 20 and 70% depending on the severity of infestation (Ngakou *et al*., 2008). Singh and Taylor (1978) pointed out that plant parts mainly attacked by thrips are flower buds and later the flowers themselves. Flower abortion is of normal magnitude in plants that are infested with thrips. Flower damage by thrips is characterized by a distortion, malformation and discoloration of the floral parts. Thrips also feed on the terminal leaf bud and bracts/stipules and cause deformation (Ezueh, 1981). Apart from the direct damage caused by thrips, it has been reported that they are vectors for a number of pathogens that they transmit mechanically from plant to plant (Ullman *et al.*, 1997).

Chemical control measures have been used and are the most widely known form of control of this pest in cowpea. However, the rapid development of insecticide resistance in thrips populations has rendered the chemical treatments ineffective (Morse and Hoddle, 2006). In addition, the cost of insecticides and proper application equipment is beyond the economic means of the majority of resource-poor farmers who grow the crop. Again, economic realities and public sensitivity to environmental degradation have currently rendered extensive insecticide use unacceptable.

1.3 JUSTIFICATION

Host plant resistance is therefore one strategy that can be identified and deployed in important cultivars to manage thrips and offers the potential to reduce or eliminate dependence on environmentally toxic chemicals that resource poor subsistence farmers cannot afford and are not well equipped to handle (Jackai and Adalla, 1997). Therefore, concerted efforts are being made to develop varieties of cowpea that are resistant to flower bud thrips to minimise the need for chemical use. Although there is evidence that low levels of resistance to flower bud thrips exists in some cowpea varieties, the desired levels of resistance have not been identified or obtained among available cowpea landraces and improved varieties. Genes from resistant cowpea varieties can therefore be incorporated through crossing into susceptible but desirable cowpea varieties to achieve more durable resistance. In addition, introgressing genes for resistance to flower bud thrips into available cowpea landraces and improved varieties will result in the availability of varieties which can be grown by farmers with minimal use of chemicals and subsequently lead to a reduction in the cost of cowpea production resulting in increased profit margin for farmers. The incorporation of flower bud thrips resistance genes into susceptible varieties requires that the inheritance pattern of the resistance trait be known.

1.4 OBJECTIVES

The objective of the study was to investigate the mode of inheritance of resistance to flower bud thrips (*Megalurothrips sjostedti*) in cowpea.

The specific objectives were:

1. To determine the contribution of maternal effects to thrips resistance.
2. To determine the types of gene action influencing the expression of the trait.
3. To determine the heritability of the trait.

CHAPTER 2

2.0 LITERATURE REVIEW

2.1 ORIGIN AND DOMESTICATION OF COWPEA

Cowpea (*Vigna unguiculata* (L.) Walp) is one of the most ancient human food sources and has probably been used as a crop plant since Neolithic times (Ehlers and Hall, 1997). A lack of archaeological evidence has resulted in contradicting views supporting Africa, Asia and South America as its origin (Summerfield *et al*., 1974; Tindall, 1983; Coetzee, 1995). One view is that cowpea was introduced from Africa to the Indian sub-continent approximately 2000 to 3500 years ago (Allen, 1983). Kitch *et al*. (1998) also reported that, the species *unguiculata* is thought to be West African Neolithic domesticated and whose progenitors were the wild weed species *dekindtiana* and *meusensis*.

The determination of the origin and domestication of cowpea had been based on morphological and cytological evidence, information on its geographical distribution and cultural practices (Ng, 1995; Ng and Maréchal, 1985). Early observations showed that the cowpeas present in Asia are very diverse and morphologically different from those growing in Africa, suggesting that both Asia and Africa could be independent centers of origin for the crop. However, Asia has being questioned as a center of origin due to the lack of wild ancestors (Ng and Maréchal, 1985). Flight (1970) reported that, the oldest archeological evidence of cowpea was found in Africa in the Kintampo rockshelter remains in Central Ghana dating about 1450–1000 BC, suggesting Africa as center of origin.

By reason of the highest genetic diversity of the crop and the presence of the most primitive form of wild cowpea, (Padulosi, 1987; 1993), Southern Africa is the most

probable center of domestication. According to Padulosi and Ng (1997), Southern Africa is the center of genetic variability because the most ancient of wild cowpea occurs in Namibia from the west, across Botswana, Zambia, Zimbabwe and Mozambique to the east, and the republic of South Africa and Swaziland to the south.

2.2 TAXONOMY

Cowpea [*Vigna unguiculata* (L) Walp.] is an annual food legume belonging to the order *Fabaceae*, subfamily *Faboideae* (Syn. *Papillionoideae*), tribe *Phaseoleae*, subtribe *Phaseolinae*, genus *Vigna*, and section Catiang (Verdcourt, 1970; Maréchal *et al*., 1978).

The genus *Vigna* is pantropical and highly variable with several species, whose exact number varies according to authors: 184 (Phillips, 1951), 170 (Faris, 1965), between 170 and 150 (Summerfield and Roberts, 1985), 150 (Verdcourt, 1970), 154 (Steele, 1976), and about 84, out of which some 50 species are indigenous to Africa (Maréchal *et al*., 1978). Verdcourt (1970) sub-divided the genus *Vigna* into eight sub-genera: *Vigna, Sigmoidotropis, Cochliasanthus, Plectotropis, Ceratotropis, Dolichovigna, Macrorhynchus and Haydonia*. Later, this classification was modified to seven sub-genera: *Vigna, Sigmoidotropis, Plectotropis, Macrorhyncha,Ceratotropis, Haydonia and Lasiocarpa* (Maréchal *et al*., 1978). All cultivated cowpeas are grouped under *V. unguiculata* sub-species *unguiculata* which is sub-divided into four semi-groups, namely *Unguiculata, biflora* (or *cylindrica*), *sesquipedalis*, and *textilis* (Ng and Maréchal, 1985).

2.3 CYTOLOGY

Cowpea is a diploid plant containing 22 chromosomes (2n=2x=22) (Timko and Singh, 2008) and its nuclear genome size is estimated to cover 620 million base pairs (Mbp) (Timko *et al*., 2008).

2.4 MORPHOLOGY AND BIOLOGY

Cowpea [*Vigna unguiculata* (L) Walp.] is a very diverse, usually glabrous, annual herb which is twinning to sub-erect and rarely erect. It has a deep taproot system with many lateral branches in the surface soil and many globular nodules. The root nodules are smooth and spherical, about 5 mm in diameter, numerous on the main taproot and its branches but sparse on the smaller roots (Chaturvedi *et al*., 2011).

The stems are striate, smooth or slightly hairy and sometimes tinged with purple. Leaves are alternate and trifoliate. The first pair of leaves is simple and opposite. Leaves exhibit considerable variation in size (6-16 x 4-11 cm) and shape (linear, lanceolate to ovate) and they are usually dark green. The leaf petiole is 5-25 cm long. The flowers are conspicuous, self-pollinating, borne on short pedicels and the corollas may be white, dirty yellow, pink, pale blue or purple in colour (Kay, 1979; Fox and Young, 1982).

According to Fery (1985), the inflorescence is axillary and formed of a peduncle 10 to 30 cm long, at the end of which there is a rachis with each node bearing a pair of flowers and a cushion of extrafloral nectaries that contribute to the attraction of insects. In cultivated forms, the flowers open at the end of the night and close in late morning, with the dehiscence of the anthers taking place several hours before the flower opens. After blooming (opening once) they wilt and collapse.

The fruit is a dehiscent pod with varying shape and length which usually shatters when dry. It is pendulous, mostly linear although curved and coiled forms occur. The pod is green at early stage and when maturing it becomes usually yellow, light brown, pink or purple. The pod length may vary from less than 11 cm to more than 100 cm (Rachie and Rawal, 1976).

Seeds of cultivated cowpea types weigh between 80 mg and 320 mg and range in shape from round to kidney-shaped. The seed coat varies in texture (such as smooth, rough, or wrinkled), colour (white, cream, green, buff, red, brown, black), and uniformity (solid, speckled, or patterned) (Timko and Singh, 2008). Seed germination is epigeal, very quick and very high.

2.5 PRODUCTION

Cowpea [*Vigna unguiculata* (L) Walp.] is an herbaceous, warm-season annual plant requiring temperatures of at least 18 ^{o}C throughout all stages of its development and having an optimal growing temperature of about 28 ^{o}C (Craufurd *et al*., 1997). It is cultivated in the tropical and subtropical regions of the world and it grows in diverse soil types and climatic conditions (Alghali, 1991). Cowpea can withstand considerable drought and a moderate amount of shade, but they are less tolerant of water-logging than soybeans. Cowpeas are short-day, warm-weather plants, sensitive to cold and killed by frost (Duke and James, 1990). According to Duke and James (1990), cowpeas can thrive on highly acid to neutral soils but they are less well adapted to alkaline soils. The crop is more tolerant of low fertility, due to its high rates of nitrogen fixation (Elawad and Hall, 1987) and effective symbiosis with mycorrhizae (Kwapata and Hall, 1985). Singh *et al*. (1987)

reported that the best cowpea yields are obtained in well-drained sandy loam to clay loam soils between pH 6 to 7.

Cowpea is cultivated in the tropics and sub-tropics covering 65 countries in Asia and Oceania, the Middle East, Southern Europe, Africa, southern USA and Central and South America (Singh *et al*., 1997). It is grown worldwide with an estimated cultivation area of about 14.5 million hectares annually and an annual worldwide production of over 4.5 million metric tons (Singh *et al*., 2002). However, the bulk of cowpea production occurs in marginal areas of West, Central, East and Southern Africa. Nigeria is the largest producer and consumer of cowpea, with about 5 million ha and over 2million mt production annually, followed by Niger (650,000 mt) and Brazil (490,000 mt) (Singh *et al*., 2002; Timko *et al*., 2008).

2.6 USES

Cowpea is a multifunctional crop, providing food for man and livestock and serving as a valuable and dependable revenue-generating commodity for farmers and grain traders (Singh 2002; Langyintuo *et al*., 2003). It can be used at all stages of its growth as a vegetable crop, and the leaves contain significant nutritional value (Nielson *et al*., 1993; Ahenkora *et al*., 1998). Like spinach, the young and tender leaves of cowpea are prepared as a pot herb (Mroso, 2003). Immature snapped pods are often mixed with other foods. The seeds are most often harvested and dried for storage and consumption at a later time, either after cooking whole or after being milled like a flour product and used in various recipes (Nielsen *et al*., 1993; Ahenkora *et al*., 1998). Innovative and appealing processed-food products using dry cowpea grain, such as cowpea-fortified baked goods, extruded snack

foods, and weaning foods, have been developed (Phillips *et al*., 2003). In livestock industries, it serves as feed when mixed with cassava (Job *et al*., 1983).

According to Bressani (1985), the mature legume contains 23-25% protein and 50-67% carbohydrate, 1.9% fats, 6.35% fibre and small percentage of the B-vitamins such as folic acid, thiamine, riboflavin and niacin as well as some micronutrients such as iron and zinc. The richness in protein makes cowpea a source of cheap plant protein (Johnson *et al*., 1983; Anderson, 1985) to people who hardly can afford animal protein derived from meat, fish, milk and eggs. Besides being low in fat and high in fiber, the protein in grain legumes like cowpea has been shown to reduce low-density lipoproteins that are implicated in heart disease (Phillips *et al*., 2003). In addition, because grain legume starch is digested more slowly than starch from cereals and tubers, their consumption produces fewer abrupt changes in blood glucose levels following consumption (Phillips *et al*., 2003). Rangel *et al*. (2004) reported that protein isolates from cowpea grains have good functional properties, including solubility emulsifying and foaming activities and could be a substitute for soy protein isolates for persons with soy protein allergies.

Cowpea is well recognized as a key component in crop rotation schemes because of its ability to help restore soil fertility for succeeding cereal crops (Tarawali *et al*., 2002; Sanginga *et al*., 2003). In addition, well-adapted, early maturing cowpea varieties capable of producing seed in as few as 55 days after planting often provide farmers with the first source of food from the current harvest sooner than any other crop (Hall *et al*., 2003). Compared to other legumes, cowpea is known to have good adaptation to high temperatures and resistance to drought stress. It contributes 30-125 Kg N/ha in the soil due

to its nitrogen fixing properties (Ennin-Kwabiah and Osei-Bonsu, 1993) and also serves as a residue, which benefits the succeeding crops. Its drought tolerance, relatively early maturity and nitrogen fixation characteristics fit very well to the tropical soils where moisture and low soil fertility is the major limiting factor in crop production (Hall, 2004; Hall *et al*., 2002). In areas facing food insecurity, such as Africa, peasants or small-scale farmers have used cowpea for intercropping with the other main crops such as maize (*Zea mays*), pearl millet *(Pennisetum glaucum)* and sorghum (*Sorghum bicolor*).

2.7 PRODUCTION CONSTRAINTS

Although cowpea is a hardy crop that can produce reasonably well under conditions that may render other crops unproductive, production is still constrained by several biotic and abiotic stresses (Hall *et al*., 1997). In the developing world where soil infertility is high, rainfall is limiting, and most of the cowpea is grown without the use of fertilizers and plant protection measures such as pesticides and herbicides, a wide variety of biotic and abiotic constraints also limit growth and severely limit yield (Singh, 2005; Timko *et al*., 2007a). The biotic factors that cause yield reduction include insect pests, parasitic flowering plants, as well as viral, fungal and bacterial diseases (Emechebe and Lagoke, 2002). The abiotic factors include poor soil fertility, drought, heat, acidity and stress due to intercropping with cereals (Singh and Tarawali, 1997; Singh and Ajeigbe, 2002). However, Terao *et al.* (1997) reported insect pests, plant diseases, parasitic flowering plants and drought to be major yield-reducing factors.

Several important pests attack cowpea throughout its growth stages from seedling until after harvest causing economic damage. The major insect pests which severely damage

cowpea during all growth stages are the cowpea aphid (*Aphis craccivora* Koch), foliage beetles (*Ootheca sp, Medythia spp*), the flower bud thrips (*Megalurothrips sjostedti* Trybom) the legume pod borer (*Maruca vitrata* Fabricius) and the sucking bug complex, of which *Clavigralla spp*, *Anoplocnemis spp*, *Riptortus spp*, *Mirperus spp*, *Nezara viridula* Fab and *Aspavia armigera* L are most important and are prevalent (Jackai and Daoust, 1986). Tremendous yield losses have been reported in Ghana, Cameroon and Nigeria (Ezueh, 1981; Ta'Ama, 1983) due to thrips infestation.

Cowpea is attacked by over 35 major diseases caused by viruses, bacteria, fungi, and nematodes (Lin and Rios, 1985; Patel, 1985). The occurrence, severity, and yield loss due to each disease and mixed infections vary from place to place, but some diseases occur and cause significant damage across the cowpea growing regions of the world (Emechebe and Florini, 1997). Virus diseases cause serious losses of yield and quality in cowpea in many cowpea growing countries. Worldwide, more than 20 viruses have been identified which infect cowpea under field or experimental conditions (Thottappilly and Rossel, 1985; Mali and Thottappilly, 1986). According to Kuhn (1990), numerous viruses are infectious to cowpea and are considered potential natural threat to cowpea production. Singh *et al*. (1984) reported that two bacterial diseases, bacterial pustule (*Xanthomonas spp*.) and bacterial blight (*Xanthomonas vignicola*), cause severe damage to cowpea worldwide. *Cercospora* leafspot, brown blotch, *Septoria* leaf spot and scab are the most common fungal diseases (Abadassi *et al*., 1987). About 55 species of nematodes have been reported on cowpea (Caveness and Ogunfowora, 1985) but the most damaging and widespread species is *Meloidogyne incognita*.

Parasitic weeds such as *Striga gesnerioides* and *Alectra vogelii* are a major limitation to cowpea production in Africa (Timko *et al*., 2007b). *Striga* causes severe damage to cowpeas in the Sudan savanna and Sahel of West Africa, whereas *Alectra* is more prevalent in the Guinea and Sudan savannas of West and Central Africa and in portions of eastern and southern Africa (Timko and Singh, 2008).

Despite cowpea being more drought tolerant than many other crops, moisture availability is still a major constraint to growth and development, especially during germination and flower setting. Erratic rainfall adversely affects both plant population and flowering ability, resulting in tremendous reduction in grain yield and total biomass in general (Timko and Singh, 2008).

2.8 ARTIFICIAL HYBRIDIZATION

The objective of hybridization is to combine desirable genes found in two or more different varieties and to produce pure-breeding progeny superior in many respects to the parental types. Cowpea is cleistogamous, producing viable pollens and receptive stigma before anthesis. This phenomenon imposes entirely self-pollination on the crop. However, for genetic improvement purpose, hand or artificial pollination is necessary. The success of artificial pollination has been reported to be low ranging from 0.5 to 50% (Rachie *et al*., 1975) and varies with genetic and physiological factors as well as the care taken in handling floral parts during the process of emasculation. The wild and weedy subspecies of cowpea hybridize easily with the cultivated forms and produce viable hybrids (Baudoin and Maréchal, 1985; Ng, 1990). But according to Rawal *et al*. (1976), the wild form could

only be used as the male parent and attempts to use it as the female parent were unsuccessful.

2.9 RESISTANCE OF PLANTS TO INSECTS

Plants represent a rich source of nutrients for many organisms including insects. Although lacking an immune system comparable to animals, plants have developed a stunning array of structural, chemical, and protein-based defenses designed to detect invading organisms and stop them before they are able to cause extensive damage (Freeman and Beattie, 2008). Plant resistance defined by Painter (1951) as "the relative amount of heritable plant qualities that influence the ultimate degree of damage suffered by the plant under a given insect pest population."

Painter (1951) described three mechanisms of plants resistance to insect pests: non-preference, antibiosis, and tolerance. Non-preference refers to a situation where a plant possesses attributes that lead to the non-use or reduced use of the plant by the insect for food, for shelter, for oviposition or for combinations of the three. Antibiosis exhibits those adverse effects on the insect's biology, behavior and/ or physiology when the insect uses resistant plant for food. Antibiosis effects are expressed in terms of weight and size of insects, sex ratio and proportion of insects entering into diapauses (Basandrai *et al*., 2011). Tolerance denotes the ability of plant to grow, repair injury or produce acceptable yield despite supporting a pest population that would normally cause significant damage and/ or kill a susceptible plant. Kogan and Ortman (1978) proposed antixenosis to describe more accurately the term of non-preference of insects for a resistant plant.

2.10 RESISTANCE OF COWPEA TO INSECTS

Due to the wide genetic variability of cowpea, much emphasis has been placed on the identification and development of insect-resistant cultivars (Singh and Jackai, 1985, Oghiakhe, *et al*., 1992). Screening methods have been developed for several major insect pests of cowpea (Ehlers and Hall, 1997). However, despite the evaluation of hundreds to thousands of cowpea accessions, plants with high levels of resistance to most of the most significant pests have not been identified. Among the pests for which good sources of resistance have been identified are the cowpea aphid (*Aphis craccivora*) and leaf hoppers (*Empoasca sp*.). Low to moderate levels of resistance have been identified in several genotypes for flower thrips, pod bugs, and Maruca pod borer (Singh *et al*., 2002; Singh, 2005).

Cowpea has been found to exhibit all the three mechanisms of resistance: antixenosis, antibiosis and tolerance. Wuttiwong *et al*. (2010) reported a strong antixenosis resistance against cowpea aphid in a resistant cowpea variety (IT82E-16). The antixenosis resistance resulted from the combination of physical and chemical features in IT82E-16 involved in aphid resistance. Singh *et al*. (2002) suggested that cowpea varieties with pigmented calyx, petioles, pods and pod tips suffer less damage from *Maruca vitrata*. A choice experiment using cowpea flowers, and olfactometer assessment, showed that IT84S-2246 was the least preferred variety, indicating evidence of antixenosis as the mechanism of resistance in this variety (Ekesi *et al*., 1998). Veerappa (1998) screened 45 cowpea lines for resistance to *Maruca* pod borer and observed that the tolerant lines had higher phenol and tannin contents compared to the susceptible lines. The high phenol and tannin contents reduced the damage of cowpea pod borer, *Maruca testulalis*. Field evaluation of cowpea cultivars for resistance to flower bud thrips showed that, IT91K-180 and Kpodjiguegue, despite

supporting a high population of thrips produced more flowers and hence more pods to compensate for the thrips damage signifying tolerance as their mechanism of resistance (Alabi *et al*., 2003). Ofuya and Akingbohungbe (1986) reported that resistance of cowpea varieties (TVu 3709, TVu 2994, BPL-3–1 and Vita 5) to black cowpea moth, *Cydia ptychora* is partly due to larval antibiosis. Ekesi *et al*. (1998) also reported that high mortality of larval stages and slower developmental rates on cowpea variety, ICV 8, indicated presence of antibiotic mechanisms of resistance. A chemical analysis of the pods of IT86D-716 was conducted to identify compounds conferring antibiosis resistance to the pod-sucking bug (PSB), *Clavigralla tomentosicollis*. Several compounds including cyanogenic heterosides, flavonoids, tannins and trypsin inhibitors were present in the pods, thus suggesting antibiosis resistance to PBS due to these compounds (Dabire-Binso *et al*., 2010). Koona *et al*. (2002) also reported TVnu 151 to exhibit antibiosis resistance to nymphs of *Clavigralla tomentosicollis*.

2.11 RESISTANCE OF COWPEA TO FLOWER BUD THRIPS

The first major insect pest of cowpea at flowering stage is the flower bud thrips, *M. sjostedti*, which is capable of causing significant grain yield reduction in the crop. In West Africa, the flower bud thrips is the most economically important thrips pest of cowpea causing yield losses between 20 and 70% depending on the severity of infestation (Ngakou *et al*., 2008). The identification of sources of resistance to flower bud thrips that can be used in breeding programs to develop resistant cowpea lines is therefore necessary to curb the situation. Singh (1977) identified two cowpea genotypes, TVu 1509 and Sanzi to possess some levels of resistance to flower bud thrips. In the screening of four cowpea genotypes (TVu 1509, Sanzi, VITA 7 and Ife Brown) for resistance to flower bud thrips,

Sanzi was found to be resistant and TVu 1509 to be moderately resistant (Omo-Ikerodah *et al*., 2009). Alabi *et al*. (2003) also reported Sanzi to be resistant to flower bud thrips in Nigeria. Screening of seventeen cowpea cultivars by Abudulai *et al*. (2006) for resistance to flower bud thrips revealed sources of resistance in Sanzi, ITH 98-45 and ITH 98-47. Alabi *et al*. (2006) categorized Sanzi as highly resistant; TVu 1509, Sewe and Moussa Local as resistant and IT90K-277-2, IT91K-180, KV × 404-8-1 and TV × 3236 as moderately resistant. TVu1509, TV × 3236, IT84S-2246, IT82D-713 & IT82D-716 have also been reported to be resistant to flower bud thrips (Salifu *et al*., 1988).

2.12 RESISTANCE OF SANZI TO FLOWER BUD THRIPS

Alabi *et al*. (2003) suggested antibiosis and/or non-preference for oviposition and/or feeding to be the basis of resistance to flower bud thrips in Sanzi and the resistance was associated with the possession of non-leafy racemes that cannot provide enough shelter for thrips because these insects have a cryptic behavior. Abudulai *et al*. (2006) reported close association between resistance to flower bud thrips and the small racemes and flowers in Sanzi suggesting antixenosis as the mechanism of resistance since the small racemes and flowers do not provide enough shelter for thrips. The non-significant differences observed in the number of days to first flower opening among four cowpea genotypes **(**TVu 1509, Sanzi, VITA 7 and Ife Brown) tested for resistance to flower bud thrips implies that, the resistance in Sanzi cannot be explained by thrips infestation escape due to early flowering (Omo-Ikerodah *et al*., 2009). However, a negative correlation between average thrips damage rating and average number of pods produced per plant suggests antibiosis or antixenosis as the basis of resistance to flower bud thrips in Sanzi (Omo-Ikerodah *et al*., 2009). In the screening of seventeen cowpea cultivars for resistance to flower bud thrips,

the low mean damage rating observed in Sanzi which correlated positively with yield loss confirms the resistance of Sanzi to flower bud thrips (Abudulai *et al*., 2006).

2.13 INHERITANCE OF RESISTANCE TO FLOWER BUD THRIPS

There is a dearth of information on the mode of inheritance of resistance to flower bud thrips in cowpea. However, studies at International Institute of Tropical Agriculture (IITA, 1983) speculated that two recessive genes control resistance to flower bud thrips. On the contrary, Omo-Ikerodah *et al*. (2000) reported that resistance to flower bud thrips may be controlled by three to five genes. In the screening for resistance to flower bud thrips in cowpea (Jackai and Singh, 1988), continuous distributions of phenotypes ranging from very susceptible to resistant were observed. This suggests that the inheritance of flower bud thrips resistance is probably quantitative. In genetic analysis of resistance to flower bud thrips in cowpea, the frequency distributions of damage rating in the segregating populations revealed that the plants were distributed over the range of both parents. This suggests that more than two genes probably control the resistance to flower bud thrips (Omo-Ikerodah *et al*., 2009). Additive × additive and dominance × dominance gene effects made major contributions to resistance to flower bud thrips (Omo-Ikerodah *et al*., 2009). Omo-Ikerodah *et al*. (2009) reported that the use of the resistant parents as female parent produces progenies with better resistance than when used as male parent. They also reported values ranging from 56% to 73.36% and 13.0% to 40.0% for broad-sense heritability and narrow-sense heritability respectively for resistance to flower bud thrips in cowpea *Vigna unguiculata* (L.) Walp.

2.14 HERITABILITY

In plant breeding, type of selection to be done and progress from selection for a particular character depends in part on the magnitude of heritability estimates. This is because the expected response under selection is a function of heritability, variation and selection intensity (Morakinyo, 1996).

Heritability is generally expressed as the proportion of the observed total variability that is genetic. In other words, selection of superior genotypes is proportional to the amount of genetic variability (Obilana and Fakorede, 1981). Thus, heritability serves as a guide to the reliability of phenotypic variability in any selection programme and hence determines its success (Hamdi, 1992). Heritability is often used in reference to the resemblance between parents and their offspring. In this context, high heritability implies a strong resemblance between parents and offspring with regard to a specific trait, while low heritability implies a low level of resemblance (Wray and Visscher, 2008).

The proportion of phenotypic differences due to all sources of genetic variance is termed broad sense heritability (h_b^2) whereas the proportion of phenotypic variance due solely to additive genetic variance is narrow sense heritability (h_n^2) (Plomin, 1990). Techniques for estimating heritability in crop plants fall into three main categories: parent-offspring regression, variance components from an analysis of variance and approximation of non-heritable variance from genetically uniform populations to estimate total genetic variance (Warner, 1952).

Mammud and Kramer (1951) concluded that heritability estimates based on regression were higher than those based on variance components. The method involves regressing the

mean value of characteristics in the progeny on the value for the same characteristics in the parent. However regression on mid-parent gives better precision than regression on one parent (Falconer, 1989).

2.15 HETEROSIS

Acquaah (2007) defined heterosis in two basic ways: better-parent heterosis and mid-parent heterosis. Better-parent heterosis is calculated as the degree by which the F_1 mean exceeds the better parent in the cross. Mid-parent heterosis is defined as the superiority of the F_1 over the means of the parents. Breeders utilize available genetic resources to modify varieties to meet the ever changing requirements. In this respect, the most important development in plant breeding of recent times is the extensive use of heterosis (Malik *et al.,* 1987). However, in self pollinated crops, the heterosis cannot be exploited directly and therefore hybrid vigor is used to identify superior hybrids as they offer more probability of developing better segregants (Sharif *et al.,* 2001).

According to Birchler *et al*. (2010), two terms are routinely used in discussing models of heterosis. One is the "dominance" model, in which recessive alleles at different loci are complemented in the hybrid, and the second is the "over-dominance" model, which posits that interactions between different alleles occur in the hybrid, leading to the increase in vigor. Charlesworth and Willis (2009) reported that the more popular of the two is the dominance concept. In the extreme version of this model, one parent contains gene copies that are missing in the opposite parent and thus the hybrid would contain more genes than either parent (Fu and Dooner, 2002).

2.16 MATERNAL EFFECT

Variation in an individual's phenotype may be determined not only by the genotype and environment of that individual but also by maternal effects, that is, the contribution of the maternal parent to the phenotype of its offspring beyond the equal chromosomal contribution expected from each parent (Roach and Wulff, 1987). Maternal effects are controlled by nuclear genes of the mother and are different from extranuclear inheritance. Extranuclear contents of the egg, however, reflect the influences of the mother's genotype and thus the pattern of inheritance becomes like that of extranuclear inheritance (Gardner and Snustard, 1981). Maternal effect results in the production of difference between reciprocal crosses, which are shown between the offspring of both sexes in all the generations where they occur.

The importance of maternal effects has long been recognized by quantitative geneticists (Dickerson, 1947), although they have largely regarded them as non-genetic environmental sources of resemblance of relatives (Falconer and Mackay, 1996; Futuyma, 1998) and a nuisance that contaminates estimates of heritability (Wade, 1998).

Non-genetic maternal effects provide a mechanism for cross-generational phenotypic plasticity and make a significant contribution to an organism's fit with the environment (Bernardo, 1996; Mousseau and Fox, 1998a, b). By modifying the offspring's phenotype or inducing the expression of new phenotypic traits, non-genetic maternal effects can also allow offspring to colonize new ecological niches and be exposed to new selective pressures. This, in turn, may result in the expression of previously unexpressed genes in the offspring that have significant phenotypic effects on their fitness (Maestripieri, 2005).

2.17 THRIPS

Thrips are small, opportunistic and ubiquitous insects of often only a few millimeters length and generally yellow, brown or black in color (Morse and Hoddle, 2006). They are mainly phytophagous, mycophagous, or predatory insects that inhabit a wide range of habitats, generally in the tropical, subtropical, and temperate regions. Their adaptive diversity has enabled successful exploitation of diverse niches, so that they have not only established themselves in a variety of plant formations, but in fungus-infested habitats such as plant litter and in bark of living and dead trees (Lewis, 1973; Mound, 1976; Bournier, 1983; Ananthakrishnan, 1984).

Thrips frequently inhabit flowers or inflorescence of various kinds, shoots, tender leaves, and fungus-infested dead or decaying wood. These insects feed on pollen as well as on spores. They are susceptible to environmental changes, and because of the polyphagous nature of many species, one can determine their abundance by the types of plant formations. They are also essential elements of the soil, occurring at depths of 10-30 cm in the soil, where some species complete their metamorphosis or hibernate (Lewis, 1973; Ananthakrishnan, 1984).

Most thrips complete their life cycle from egg to adult stage in two to three weeks. The duration varies with the host and with abiotic factors such as temperature and humidity (Andrewartha, 1971). For flower bud thrips, Salifu (1992) reported that development from egg to adult takes about 19 days at 29°C and 58% RH and adults live for about 23 days. Rapid breeding, laying eggs on leaf petioles, peduncles, inflorescences and pods was also reported in flower bud thrips by Tamo *et al*. (1993).

Thrips can contaminate a wide variety of commodities and human devices because of their small size, ability to build to high numbers, cryptic behavior, egg deposition inside plant tissue and a propensity to secrete themselves in tight spaces (Morse and Hoddle, 2006).

2.17.1 FLOWER BUD THRIPS (*MEGALUROTHRIPS SJOSTEDTI*)

The cowpea flower thrips, *Megalurothrips sjostedti*, occurs throughout tropical Africa and causes yield losses of up to 100% in Tanzania, Ghana, Cameroon, and Nigeria (Agyen-Sampong, 1978; Singh and Taylor, 1978; Ezueh, 1981; Price *et al*., 1983; Ta'Ama, 1983). Adult thrips, which are shiny black, minute insects, are found feeding in flower buds and flowers (Singh and van Emden, 1978). During the pre-flowering period, *M. sjostedti* nymphs and adults may damage the terminal leaf buds and bracts/stipules, causing the latter to become deformed with a brownish yellow mottled appearance (Ezueh, 1981). However, the principal point of plant attack is on the flower buds and, later, on the flowers themselves (Singh and Taylor, 1978). Attacked flower buds become brown and eventually abort (Singh, 1977), leaving behind dark red scars (Akingbohungbe, 1982). Flower damage is characterized by a distortion, malformation, and discoloration of floral parts (Singh and Taylor, 1978). Flower thrips populations are higher during the dry season, which favors rapid multiplication of thrips (Agyen-Sampong, 1978; Ezueh, 1981). When the thrips population is very high, open flowers are distorted and discolored. Flowers fall early with the result that pods are not formed (Singh and van Emden, 1978). Apart from the direct damage caused by thrips, it has been reported that they are vectors for a number of pathogens that they transmit mechanically from plant to plant (Ullman *et al.,* 1997).

This study sought to investigate the nature of inheritance of resistance to flower bud thrips in cowpea in order to incorporate the best available level of resistance to this pest into improved cowpea varieties to reduce the cost of cowpea production resulting in increased profit margin for farmers.

CHAPTER 3

3.0 MATERIALS AND METHODS

3.1 EXPERIMENTAL SITE

The experiment was conducted at Crops Research Institute (CRI), Fumesua, Ghana.

3.2 EXPERIMENTAL MATERIALS

A cowpea genotype, Sanzi that has been identified as possessing some level of resistance to flower bud thrips (*Megalurothrips sjostedti*) and Bengpla, a susceptible genotype, were used as test materials. Seeds of Sanzi and Bengpla were obtained from CRI, Fumesua, Ghana.

3.2.1 GENOTYPE 1 – SANZI

Sanzi is a landrace from Ghana and has been identified with moderately high resistance to flower bud thrips (Alabi *et al*., 2003; Abudulai *et al*., 2006; Omo-Ikerodah *et al*., 2009). Sanzi matures between 55 and 60 days after planting (DAP) and is considered an extra-early maturing variety. It is a semi-prostrate variety with small-size seeds and black testa.

3.2.2 GENOTYPE 2 – BENGPLA

Bengpla is an early maturing (65 d) variety with erect growth habit, medium-size broad leaves, and long upright peduncles. It has medium-size seeds (16 g/100 seeds) with smooth white shiny testa and black hilum. It has a mean grain yield of about 1,023 kg/ha and a potential of 1.8 tons/ha. It has 29.75% protein and 1.91% oil. Despite all these important attributes, Bengpla has been observed to be susceptible to flower bud thrips at CRI, Fumesua in the Ashanti Region of Ghana (S. Addy, personal communication). However,

farmers and consumers prefer Bengpla to Sanzi because of its white smooth bold seed, shorter cooking time, and excellent taste.

3.3 METHODOLOGY

The experiment was conducted in three stages. The first and second stages were carried out in plastic pots under full insecticide protection from July to December, 2011 and the third stage in the field under natural infestation of thrips from February to May, 2012.

3.3.1 STAGE 1

In the first stage, the two parental genotypes were grown and direct and reciprocal crosses made to produce F_1 plants and their reciprocals. i.e., Sanzi × Bengpla (F_1) and Bengpla × Sanzi (F_1 reciprocal).

3.3.2 STAGE 2

In the second stage, two F_1 seeds (F_1 and RF_1) were planted to produce F_2 progenies and at the same time backcrossed to their respective parents. The genotypes obtained during the second stage were as follows:

1. (Sanzi × Bengpla) × Sanzi - Backcross one (BC_1)
2. (Sanzi × Bengpla) × Bengpla - Backcross two (BC_2)
3. (Bengpla × Sanzi) × Sanzi - Reciprocal backcross one (RBC_1)
4. (Bengpla × Sanzi) × Bengpla - Reciprocal backcross two (RBC_2)
5. Sanzi × Bengpla - F_2
6. Bengpla × Sanzi - F_2 reciprocal (RF_2)

To synchronize the period of flowering, the planting dates of the parental genotypes were staggered. The extra-early maturing genotype, Sanzi was planted three days after planting

Bengpla which was early maturing. Plastics pots measuring 24 cm at the top and 15 cm at the base with 21 cm height were used. The plastic pots were filled with sterilized top soil.

The potted plants were watered daily using watering can throughout the growth period. Weeds were controlled by hand pulling as and when necessary throughout the growing period of the plants. The plants were sprayed four times at 14 DAP, 30 DAP, 40 DAP and 50 DAP to control aphids (*Aphis craccivora*), flower bud thrips (*Megalurothrips sjostedti*) and a complex of pod sucking bugs. The insecticides used were Karate (600 ml/ha) and Cymethoate (1000 ml/ha) for pre- and post-flowering insect pests control respectively.

3.3.3 STAGE 3

In the third stage, seeds of the following genotypes were sown in randomized complete blocks replicated three times to evaluate them for resistance to flower bud thrips, *Megalurothrips sjostedti* under natural infestation in the field.

S/N	GENOTYPES
1.	Sanzi – P_1
2.	Bengpla – P_2
3.	Sanzi × Bengpla – F_1
4.	Bengpla × Sanzi - F_1 reciprocal (RF_1)
5.	(Sanzi × Bengpla) × Sanzi - Backcross one (BC_1)
6.	(Sanzi × Bengpla) × Bengpla - Backcross two (BC_2)
7.	(Bengpla × Sanzi) × Sanzi - Reciprocal backcross one (RBC_1)
8.	(Bengpla × Sanzi) × Bengpla - Reciprocal backcross two (RBC_2)
9.	Sanzi × Bengpla - F_2
10.	Bengpla × Sanzi - F_2 reciprocal (RF_2)

The field experiment was conducted under irrigation during the dry period, covering the months of February to April, 2012 and under rain-fed in May, 2012. The genotypes were grown in a randomized complete block design with three replications. Each replicate consisted of one plot of each of the parents, F_1 and RF_1, two plots of each backcross and six plots of each F_2 and RF_2 generations. Each plot was made up of a row, 2 m long with 0.6 m between rows and 0.2 m within plants giving 10 plants per row.

Increase populations of flower bud thrips on test plants were achieved by planting Bengpla, a susceptible cultivar as spreader rows in a checker board design two weeks prior to planting the test plants (Alabi *et al*., 2003). At the raceme stage of the test plants, the spreader row plants (Bengpla) were uprooted and laid between rows of the test plants (Alabi *et al*., 2003; Omo-Ikerodah *et al*., 2009). This caused the thrips to move away from the drying plants to the test plants.

The test plants were sprayed at 14 DAP and 57 DAP against aphids and pod-sucking bugs respectively to eliminate their confounding effects in identifying thrips resistant genotypes. Hand weeding was carried out at three and six weeks after planting.

3.4 CROSSING PROCEDURE

The crossing procedure used by Rachie *et al*., (1975) was followed which consists of emasculation, in the evening of the plants flower buds which will open the following morning and to be used as female parent and applying pollen of the male parent directly to the stigma of the emasculated parent the following morning. Emasculation was done with sharply pointed forceps sterilized with alcohol between emasculations to prevent

contamination by unwanted pollen. After emasculation, the stigmatic surface was checked for the presence of pollen before cross pollination was attempted. The flower chosen as a source of pollen was held between the thumb and the forefinger with the standard and wing folded back to expose the pollen. This was then used as “brush” to apply pollen to the emasculated flower. Tags (indicating the cross and date) were affixed to the raceme beneath the pollinated bud to identify the cross and date of cross.

3.5 PARAMETERS MEASURED

1. Thrips damage rating (Jackai and Singh, 1988).
2. Thrips population.
3. Days to 50% flowering.

3.6 THRIPS DAMAGE RATING

Test plants were carefully inspected for flower bud thrips damage such as browning/drying of stipules, leaf or flower buds and abscission with minimal disruption to the plants and damage rated on a scale of 1-9 at 35 days after planting and subsequently at weekly intervals for four weeks (Jackai and Singh, 1988). The scale ranged from 1 to 9, with 1 as highly resistant, 3 as resistant, 5 as moderately resistant, 7 as susceptible and 9 as highly susceptible (Table 1).

Table 1. **Scale for rating flower bud thrips infestation on cowpea**

Rating	Appearance
1	No browning/drying (i.e. scaling) of stipules, leaf or flower buds; no bud abscission
3	Initiation of browning of stipules, leaf or flower buds; no bud abscission
5	Distinct browning/drying of stipules and leaf or flower buds; some bud abscission
7	Serious bud abscission accompanied by browning/drying of stipules and buds; non elongation of peduncles
9	Very severe bud abscission, heavy browning, drying of stipules and buds; distinct non-elongation of (most or all) peduncles.

Source: Jackai and Singh (1988)

3.7 THRIPS POPULATION

Population densities of flower bud thrips were estimated by randomly picking 10 racemes and flowers from each genotype. The flowers and racemes were placed separately in labeled glass vials containing 40% ethanol and subsequently were dissected to count thrips (Abudulai *et al*., 2006).

3.8 STATISTICAL AND GENETIC ANALYSES

The statistical package used was GenStat discovery edition (version 4). Thrips counts were Log transformed for statistical analysis. Data for thrips population and days to 50% flowering were subjected to analysis of variance (ANOVA). Restricted Maximum Likelihood (REML) variance components analysis was also used to analyze data for thrips damage rating taken weekly for four weeks. Since data in a repeated measure are

dependent and correlated, REML variance components analysis provides an effective analysis for repeated measurements. It involves the use of mixed models approach to test the significance of week factor, generation factor and interaction between week and generation. Where the difference was significant ($p < 0.05$) treatment means were separated using Least Significant Difference (LSD) test at 5%.

Generation mean analysis (GMA) was carried out to determine the types of gene action influencing the expression of flower bud thrips resistance trait. The additive-dominance model was adopted in the estimation of gene effects for thrips damage rating. The adequacy of the model in explaining the mode of inheritance of resistance to flower bud thrips in cowpea was examined by two tests:

1. The scaling tests A, B and C of Mather (Mather, 1949)
2. The joint scaling test of Cavalli (Cavalli, 1952)

The scaling tests of Mather (Mather, 1949) involve testing the parameters A, B and C for their deviation from zero. If the model is adequate, parameters A, B and C will each equals to zero within the limits of sampling error. Values of the individual tests A, B and C and their corresponding standard errors (SE) were calculated using the following formulas:

$A = 2BC_1 - P_1 - F_1$ $\quad SE_A = \sqrt{V_A}$ $\quad V_A = 4V_{BC1} + V_{P1} + V_{F1}$

$B = 2BC_2 - P_2 - F_1$ $\quad SE_B = \sqrt{V_B}$ $\quad V_B = 4V_{BC2} + V_{P2} + V_{F1}$

$C = 4F_2 - 2F_1 - P_1 - P_2$ $\quad SE_C = \sqrt{V_C}$ $\quad V_C = 16V_{F2} + 4V_{F1} + V_{P1} + V_{P2}$

where BC_1, BC_2, P_1, P_2, F_1, and F_2 are the generation means and V is variance.

Testing of the parameters (A, B and C) was done using t-test and the appropriate tests of significance are:

$tA = A/ SE_A$

$tB = B/ SE_B$

$tC = C/ SE_C$

where tA, tB and tC are the calculated t values. The significance of the parameters (A, B and C) was checked by comparing the calculated t values with the tabulated t values at the appropriate degrees of freedom (df). The number of degrees of freedom was determined by summing up the individual df for each of the generations involved in the calculation of a given parameter. When the t calculated is larger than the t value (5%) from the t table, then the deviation is significantly different from zero.

The joint scaling test (using weighted least square procedure), proposed by Cavalli (1952), effectively combines the whole set of scaling tests (A, B and C) into one and this offers a more general and more convenient approach. It consists of estimating parameters m (mid-parent value), [d] (additive) and [h] (dominance) from the means of available types of generations in a generalized inverse equation matrix followed by a comparison of these means as observed with their expected values derived from the estimates of the three parameters. The goodness of fit of the three-parameter model (mid-parent (m), additive [d] and dominance [h] effects) was tested statistically by squaring the deviation of the observed from the expected value for each generation and by multiplying by the corresponding weight (reciprocal of the variance of generation mean [$1/ V_X$]). The sum of the products over the six generations is the calculated chi-square (χ^2). Since the data comprise of six observed means (P_1, P_2, F_1, F_2, BC_1 and BC_2), and three parameters (m, [d]

and [h]) have been estimated, the degrees of freedom for the joint scaling test are derived from the difference between the number of the generations and number of the estimated parameters (6-3=3). Inadequacy of the additive-dominance model is revealed by a significant χ^2, and by one or more of the individual scaling tests (A, B and C) showing a significant departure from zero.

Inadequacy of the additive-dominance model is an indication that more complex factors (non-allelic interaction or epistasis) are involved in the inheritance (Mather and Jinks, 1982). When this happens, the original data is transformed to normalize the distribution in the non-segregating populations (Mather and Jinks, 1982) and the adequacy of the model is re-tested.

3.9 HERITABILITY AND HETEROSIS ESTIMATES

Broad sense and narrow sense heritabilities were calculated using the variances of the parents, F_1, F_2, and backcross generations (BC_1 and BC_2) to estimate phenotypic (V_P), environmental (V_E), total genetic (V_G), additive genetic (V_A) and dominance genetic (V_D) variances,

where:

$V_P = V_{F2}$

$V_E = (V_{P1} + V_{P2} + V_{F1})/ 3$

$V_G = V_{F2} - V_E$

$V_A = 2(V_{F2}) - V_{BC1} - V_{BC2}$

$V_D = V_{BC1} + V_{BC2} - V_{F2} - V_E$

Broad sense heritability = $h_b^2 = (V_A + V_D)/ V_{F2}$, where $V_A + V_D$ represent the genetic variance of F_2 (Allard, 1960), while narrow sense heritability = $h_n^2 = V_A/ V_{F2}$ (Warner, 1952).

Mid-parent heterosis was estimated as the percentage deviation of the mean F_1 value from the mid-parent value.

CHAPTER 4

4.0 RESULTS

4.1 Progenies of crosses

From Table 2, no significant ($p > 0.05$) differences were observed among the generations in the number of days to 50% flowering and thrips population.

Table 2. **Mean number of days to 50% flowering and thrips population in ten generations of direct and reciprocal cowpea crosses**

Generation	Days to 50% flowering	Thrips population
Sanzi (P_1)	41.67	2.07
Bengpla (P_2)	42.33	2.40
$P_1 \times P_2$ (F_1)	41.67	2.01
$P_2 \times P_1$ (RF_1)	42.00	2.08
$F_1 \times P_1$ (BC_1)	41.33	2.11
$RF_1 \times P_1$ (RBC_1)	40.33	1.98
$F_1 \times P_2$ (BC_2)	41.00	2.06
$RF_1 \times P_2$ (RBC_2)	41.67	2.23
$F_1 \times F_1$ (F_2)	40.00	2.10
$RF_1 \times RF_1$ (RF_2)	40.00	2.38
LSD (5%)	1.835	0.304
CV (%)	2.60	8.30

Values are means of three replicates. NS = F-test not significant at p = 0.05.

Table 3. **Analysis of deviance for thrips damage scores across four weeks in ten generations of direct and reciprocal cowpea crosses**

Fixed term	Wald statistic	n.d.f	F statistic	d.d.f
Generation	219.32	9	24.37***	80.0
Week	22.79	3	7.60***	80.0
Generation × Week	12.92	27	0.48^{ns}	80.0

n.d.f. = numerator degrees of freedom, d.d.f = denominator degrees of freedom, F statistic = Wald statistic/ n.d.f, *** = Significant at $p < 0.001$, $ns = F$ -test not significant at p = 0.05. d.d.f for approximate F-tests are calculated using algebraic derivatives ignoring fixed/boundary/singular variance parameters.

4.2 Restricted Maximum Likelihood (REML) variance components analysis

Analysis of deviance across four weeks of thrips damage rating indicated highly significant ($p < 0.001$) differences among the ten generations and weeks. However, a non-significant ($p > 0.05$) generation × week interaction was observed for thrips damage expression (Table 3). The results (Table 3 and Figure 1) revealed that, number of weeks had no effect on the responses of the generations to thrips infestation therefore week 2, where the highest damage was recorded (Figure 1), was chosen for further analysis.

4.3 Responses of generations to thrips infestation

As plants matured, the damage caused by thrips increased from week 1 to week 2 in all the generations, remained stable from week 2 to week 3 and decreased from week 3 to week 4 in most of the generations (Figure 1). Bengpla consistently had the highest damage scores while Sanzi had the lowest damage scores across the weeks (Figure 1). Thrips damage scores for all the generations were intermediate between the two parents (Sanzi and Bengpla) but were skewed towards the parent with lower damage score (Figure 1). In

contrast to Bengpla, thrips damage scores for Sanzi decreased significantly from week 3 to week 4 (Figure 1).

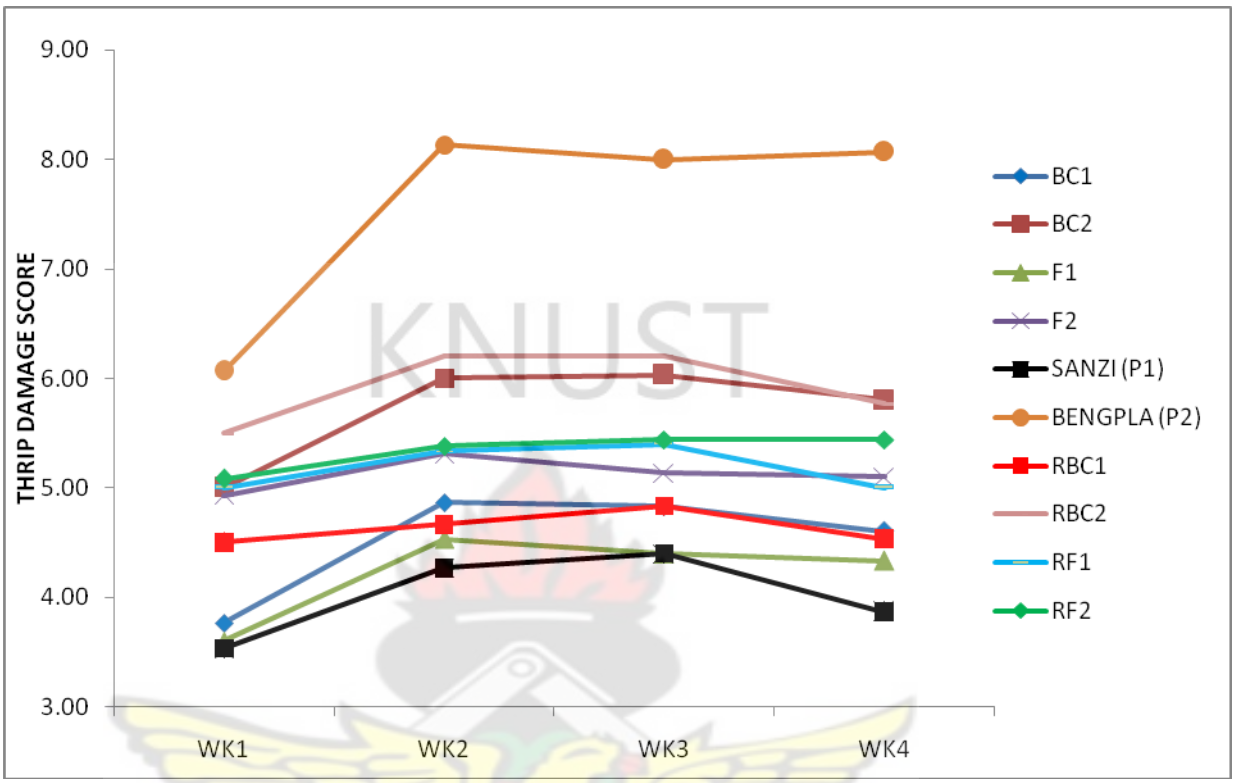

Figure 1. **Thrips damage scores over time for ten generations of direct and reciprocal cowpea crosses**

4.4 Thrips damage scores of generations

The means, standard errors and variances of thrips damage scores of the six basic generations of Sanzi × Bengpla and their reciprocals are presented in Table 4. The results showed that Sanzi had significantly lower damage score than Bengpla. The mean of the F_1 was less than the mid-parent value but higher than the mean of the parent with lower damage score (P_1). The RF_1 hybrid also had mean thrips damage score lower than that of P_2 (parent with higher damage score) but closer to that of P_1 (Table 4). The difference between the means of the direct and reciprocal crosses was not significant (Table 4); so the values were pooled for subsequent computations (Table 5).

Table 4. **Means (± SE) and variances of thrips damage scores in ten generations of direct and reciprocal cowpea crosses**

Generation	Number of plants	Mean	Variance
Sanzi (P_1)	30	4.27 ± 0.18d	0.96
Bengpla (P_2)	30	8.13 ± 0.18a	1.02
Mid-parent		6.20	
$P_1 \times P_2$ (F_1)	30	4.53 ± 0.28d	2.40
$P_2 \times P_1$ (RF_1)	30	5.33 ± 0.26bcd	1.95
$F_1 \times P_1$ (BC_1)	60	4.87 ± 0.15cd	1.34
$RF_1 \times P_1$ (RBC_1)	60	4.67 ± 0.15d	1.38
$F_1 \times P_2$ (BC_2)	60	6.00 ± 0.17bc	1.69
$RF_1 \times P_2$ (RBC_2)	60	6.20 ± 0.17b	1.65
$F_1 \times F_1$ (F_2)	360	5.31 ± 0.06bcd	1.32
$RF_1 \times RF_1$ (RF_2)	360	5.38 ± 0.07bcd	1.85

Means followed by the same letter(s) are not significantly different at p = 0.05.

R = Reciprocal.

Table 5. **Pooled means (± SE) and variances of thrips damage scores in Sanzi × Bengpla cross**

Generation	Number of plants	Mean	Variance
Sanzi (P_1)	30	4.27 ± 0.18	0.96
Bengpla (P_2)	30	8.13 ± 0.18	1.02
Mid-parent		6.20	
F_1	60	4.93 ± 0.20	2.30
BC_1	120	4.77 ± 0.11	1.36
BC_2	120	6.10 ± 0.12	1.67
F_2	720	5.34 ± 0.05	1.58

BC_1 = Progeny of a cross between F_1 and P_1

BC_2 = Progeny of a cross between F_1 and P_2.

4.5 Generation mean analysis

The observed values of all the generation means along with standard errors, variances, variances of the means, the number of plants on which the means and variances were based and coefficient of variation are shown in Table 6. It was possible to assess whether the variation observed in the generation means could be explained on an additive-dominance basis or whether the interaction between genes at different loci (epistasis) was important. This was achieved by using the A, B and C scaling tests proposed by Mather (1949) and Joint scaling test of Cavalli (1952) for the detection of non-allelic interaction. The A, B and C scaling and Joint scaling tests were estimated from Table 6. Inadequacy of the model was revealed by a significant χ^2, and by one of the individual scaling tests (A) showing a significant departure from zero at p = 0.05 (Table 7).

Table 6. **Generation mean (X) along with standard error (SE), no. of plants, Variance (Vx), variance of the mean (V_x) and coefficent of variation (CV %) for thrips damage score in six generations of a cowpea cross**

Generation	Mean (X) ± SE	No. of plants	Variance (Vx)	Variance of Mean (V_x)	CV (%)
Bengpla	8.13 ± 0.18	30	1.02	0.034	12.39
Sanzi	4.27 ± 0.18	30	0.96	0.032	22.97
Mid-parent	6.20				
F_1	4.93 ± 0.20	60	2.30	0.038	30.75
F_2	5.34 ± 0.05	720	1.58	0.002	23.55
BC_1	6.10 ± 0.12	120	1.67	0.014	21.19
BC_2	4.77 ± 0.11	120	1.36	0.011	24.44

BC_1 = Progeny of a cross between F_1 and the higher parent

BC_2 = Progeny of a cross between F_1 and the lower parent

The results showed that Mather's (1949) scaling test A was significant whiles scaling tests B and C were not significantly different from zero at P = 0.05 (Table 7). The values of A and C were negative whereas B was positive.

In the joint scaling test of Cavalli (1952), the Chi-square test value was significantly different from zero at p = 0.05 (Table 7), which perhaps suggests the presence of non-allelic interaction in the inheritance of resistance to flower bud thrips. The dominance [h] component was negative and the magnitude of additive [d] component was greater than that of [h].

Table 7. **A, B and C scaling and joint scaling tests for thrips damage scores of cross Bengpla × Sanzi**

Scaling test (Mather, 1949)	Values ± SE
A	-0.86 ± 0.358*
B	0.34 ± 0.338^{ns}
C	-0.90 ± 0.500^{ns}
Joint scaling test (Cavalli, 1952)	
Mid-parent m	6.09 ± 0.110*
Additive [d]	1.68 ± 0.100*
Dominance [h]	-1.40 ± 0.216*
χ^2 3df	12.79*

χ^2 = Chi-square for testing the adequacy of the additive-dominance model

ns = Not significantly different from zero at p = 0.05

* = Significantly different from zero at p = 0.05

The original data were square-root transformed (Table 8) to restore the genes to independence which satisfies the assumptions of the additive-dominance model and adequacy re-tested (Table 9). When the original data were transformed, Mather's (1949) A, B and C scaling tests were not significantly different from zero at p = 0.05. However, the values of A and C were negative whereas B was positive (Table 9).

Table 8. **Generation mean (X) along with standard error (SE), no. of plants, Variance (Vx), variance of the mean (V_x) and coefficent of variation (CV %) for thrips damage score (square-root transformed) in six generations of a cowpea cross**

Generation	Mean (X) ± SE	No. of plants	Variance (Vx)	Variance of Mean (Vx)	CV (%)
Bengpla	2.85 ± 0.03	30	0.03	0.0010	6.27
Sanzi	2.05 ± 0.05	30	0.06	0.0020	12.04
Mid-parent	2.45				
F_1	2.19 ± 0.04	60	0.12	0.0020	15.87
F_2	2.30 ± 0.01	720	0.08	0.0001	12.04
BC_1	2.46 ± 0.02	120	0.07	0.0006	10.74
BC_2	2.17 ± 0.02	120	0.07	0.0006	12.61

BC_1 = Progeny of a cross between F_1 and the higher parent

BC_2 = Progeny of a cross between F_1 and the lower parent

In the joint scaling test of Cavalli (1952), the values of m, [d] and [h] were significantly different from zero at p = 0.05. The dominance [h] component was negative and the magnitude of additive [d] component was greater than that of [h]. The Chi-square value was however not significantly different from zero (Table 9) indicating the adequacy of the additive-dominance model.

Table 9. **A, B and C scaling and joint scaling tests for thrips damage scores (square-root transformed) in cross Bengpla × Sanzi**

Scaling test (Mather, 1949)	Values ± SE
A	-0.12 ± 0.073^{ns}
B	0.10 ± 0.080^{ns}
C	-0.08 ± 0.112^{ns}
Joint scaling test (Cavalli, 1952)	
Mid-parent m	2.45 ± 0.023*
Additive [d]	0.36 ± 0.021*
Dominance [h]	-0.29 ± 0.047*
χ^2 3df	7.49^{ns}

χ^2 = Chi-square for testing the adequacy of the additive-dominance model

ns = Not significantly different from zero at p = 0.05

* = Significantly different from zero at p = 0.05

4.6 Heritability and heterosis estimates

Broad sense and narrow sense heritabilities and heterosis (based on mid-parent value) for flower bud thrips resistance are presented in Table 10. From the original data, 9.49%, 8.23% and (-) 20.48% were recorded for broad sense, narrow sense and heterosis respectively. The square-root transformed data gave 12.5%, 25% and (-) 10.61% for broad sense, narrow sense and heterosis respectively.

Table 10**. Percentage heritability and heterosis of flower bud thrips resistance in a cowpea cross**

Data	Heritability (%)		Heterosis (%)
	Broad sense	Narrow sense	
Original	9.49	8.23	-20.48
Square-root transformed	12.50	25.00	-10.61

Heterosis estimate based on mid-parent value

CHAPTER 5

5.0 DISCUSSION

From the study conducted, no significant differences were observed among the generations in thrips population. This presupposes that, although the experiment was not conducted under controlled conditions, almost the same number of thrips was imposed on the generations to cause the damage. Therefore any differences observed among the generations in damage rating can be attributed to the different degrees of resistance exhibited by the generations as suggested by Alabi *et al*. (2003).

The generations did not differ significantly in the number of days to 50% flowering. Thus, the resistance manifested in the generations cannot be attributed to thrips infestation escape due to early flowering as postulated by Omo-Ikerodah *et al*. (2009).

Variation in damage was observed in the parents. Bengpla consistently had the highest damage scores while Sanzi had the lowest damage scores across the four weeks. Genotypic differences in thrips damage score were probably related to the inherent resistance and susceptibility of Sanzi and Bengpla respectively. Sanzi has been reported to be resistant to flower bud thrips (Alabi *et al*. 2003; Abudulai *et al*., 2006; Omo-Ikerodah *et al*., 2009) which confirms the results from the study. Bengpla was also observed to be susceptible to thrips in Fumesua in the Ashanti Region of Ghana (S. Addy, personal communication) which also agrees with the observations made from the study.

The characteristic symptoms of flower bud thrips damage include browning and drying of stipules, leaf or flower buds, non-elongation of peduncles and flower bud abscission leading to no or very few pod production. These characteristics were expressed in varying degrees in the segregating generations. The continuous distribution of flower bud thrips damage scores displayed by the segregating generations revealed that, in most of the cases,

the plants were distributed over a range of both parents (Figure 1). This suggests quantitative inheritance for resistance to flower bud thrips. These observations are in conformity with similar observation (Jackai and Singh, 1988) that inheritance of flower bud thrips resistance is quantitative. According to Omo-Ikerodah *et al*. (2009), more than two genes control resistance to flower bud thrips which corroborates the results obtained. The segregating generations were skewed towards the parent with lower damage score (P_1) suggesting that dominance genes controlled flower bud thrips resistance.

There was no significant difference between means of direct and reciprocal crosses. So the cytoplasmic influence on the trait expression as detected by Omo-Ikerodah *et al*. (2009) was not realized in this study. This suggests that the genes controlling flower bud thrips resistance were all nuclear and cytoplasmic genes had no effect on the inheritance of flower bud thrips resistance.

The mean thrips damage score of the F_1 was less than the mid-parent value and closer to the mean of the parent with lower damage score (P_1) indicating dominance of resistance over susceptibility. This result also implies negative heterosis (towards the parent with lower damage score) for resistance to flower bud thrips.

In the generation mean analysis, Mather's (1949) A, B and C scaling tests and the joint scaling test of Cavalli (1952) were significantly different from zero indicating the inadequacy of the additive-dominance model in explaining the mode of inheritance of resistance to flower bud thrips. This therefore suggests the presence of digenic epistasis for flower bud thrips resistance (Mather and Jinks, 1982).

When this happens, Mather and Jinks (1982) suggested a transformation on the original data to normalize the distributions in the non-segregating populations. Upon transformation, however, the additive-dominance model was found adequate by a non-significant χ^2, and by individual scaling tests, A, B and C showing a non-significant departure from zero. These results are in contrast to the findings of Omo-Ikerodah *et al*. (2009), who found the additive-dominance model to be inadequate to explain the gene action involved in the inheritance of resistance to flower bud thrips. The adequacy of the additive-dominance model indicated the absence of digenic epistasis for flower bud thrips resistance.

The additive-dominance model revealed that both additive and dominance gene effects contributed significantly to the inheritance of resistance to flower bud thrips. However, additive gene effect was larger than dominance gene effects. According to Cukadar-Olmedo and Miller (1997), the sign for dominance effect is a function of the F_1 mean value in relation to the mid-parental value and indicates which parent is contributing to the dominance effect. Therefore, the negative sign of dominance indicates dominance in the direction of the parent with lower thrips damage score. The large contribution of additive effect to flower bud thrips resistance suggests effective selection for the trait as proposed by Acquaah (2007). Whereas dominance gene action would favor the production of hybrids, additive gene action signifies that standard selection procedures would be effective in bringing about advantageous changes in character (Edwards *et al.*, 1975). These observations indicate that effective selection for genetic improvement of the trait could be achieved through repeated selection of desirable recombinants from the segregating population. Lamkey and Lee (1993) suggested reciprocal recurrent selection as

a method of crop improvement for the contribution of both additive and dominance gene effects to the expression of a trait. The results from the study are inconsistent with the findings of Omo-Ikerodah *et al*. (2009) who reported the predominance of dominance and epistasis for flower bud thrips resistance.

Broad and narrow sense heritabilities for flower bud thrips resistance estimated from both original and transformed data were generally low indicating large effect of the environment on the trait. On the contrary, however, Omo-Ikerodah *et al*. (2009) found high broad sense heritability for flower bud thrips resistance. According to Acquaah (2007), the action of minor genes is small and significantly influenced by the environment. The low heritability estimates observed can therefore be attributed to the action of minor genes on the expression of the trait. Also, Timko and Singh (2008) reported that most insect resistance factors in cowpea do not provide immunity to the pest and often have low heritability under field conditions which explains the low heritabilities obtained. Low heritability of the trait suggests that lower selection pressure should be imposed in order to advance as many high-potential recombinants as possible in a hybridization programme (Acquaah, 2007). Negative heterosis over mid-parent was observed for thrips resistance score indicating heterosis in the direction of the better parent (parent with lower damage score).

CHAPTER 6

6.0 CONCLUSION AND RECOMMENDATION

6.1 CONCLUSION

The study has shown that it is possible to incorporate resistant genes into susceptible but desirable cultivars through crossing. This is evident from the fact that the segregating generations were intermediate between the resistant and susceptible parents and were skewed towards the resistant parent.

The non-significant difference between direct and reciprocal crosses suggests that genes controlling resistance to flower bud thrips were all nuclear and cytoplasmic genes had no effect on the inheritance of resistance to flower bud thrips.

The study revealed that additive and dominance gene action contributed significantly to the inheritance of resistance to flower bud thrips therefore measures to improve the trait should focus on simple selection and hybridization procedures.

The low heritability shows the influence of environment on the trait and therefore suggests that lower selection pressure should be imposed in order to advance as many high-potential recombinants as possible in a hybridization programme.

6.2 RECOMMENDATION

Backcross breeding should be complemented with marker assisted selection to enhance the efficiency and effectiveness of thrips resistance breeding.

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APPENDICES

Appendix 1

Analysis of variance

Variate: DAYS_TO_50%_FLOWERING

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
BLOCK stratum	2	13.400	6.700	5.85	
BLOCK.*Units* stratum					
TREATMENT	9	18.800	2.089	1.83	0.133
Residual	18	20.600	1.144		
Total	29	52.800			

Appendix 2

Analysis of variance

Variate: THRIPS_POPULATION

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.
BLOCK stratum	2	0.20637	0.10318	3.28	
BLOCK.*Units* stratum					
TREATMENT	9	0.59545	0.06616	2.10	0.086
Residual	18	0.56675	0.03149		
Total	29	1.36857			