

Research Application Summary

Evaluation of biochemical components as a mechanism of cassava resistance to whitefly infestation in Uganda

Mwila, N.,^{1*} Rubaihayo, P.,¹ Kyamanywa, S.,¹ Odong, T.,¹ Nuwamanya, E.² & Mwala, M.³

¹College of Agricultural and Environmental Sciences, Department of Agricultural Production, Makerere University, P. O. Box 7062, Kampala, Uganda

²National Agricultural Crops Resources Research Institute (Namulonge), P.O. Box 7084, Kampala, Uganda

³Department of Plant Science, University of Zambia, P. O. Box 32379, Lusaka, Zambia

*Corresponding author: mwilanatasha@yahoo.co.uk

Abstract

Bemisia tabaci is one of the most common whitefly species worldwide that have been identified to cause serious harm in various crops through direct damage and as a vector of viral diseases. In Uganda, cassava varieties used have succumbed to the ever increasing populations of the pest and have resulted in severe damage and epidemics. Through complex interactions with the plant, the pest feeds by tapping into the phloem of plant and as it maneuvers on the plant is reported to minimize plant defense responses. A number of cassava varieties have exhibited low populations of the pest and low damage levels worldwide. Although several metabolite components have been shown to be present in some cassava varieties, the resistance mechanisms operating in cassava to *B. tabaci* have not been well understood. The changes that occur in metabolite content as a result of the interaction with *B. tabaci* and their effect on crop resistance to the pest have not been well elucidated. It is therefore critical that knowledge is generated on the metabolites in cassava that may be associated with *B. tabaci* resistance as a means for enhancing breeding of resistant cassava genotypes. This review article presents a summary on cassava resistance to *B. tabaci* research status and the development of breeding research in Uganda.

Key words: Cassava, resistance mechanisms, secondary metabolites, *B. tabaci*, Uganda

Résumé

Bemisia tabaci est l'une des espèces d'aleurodes les plus répandues dans le monde et est connue pour le préjudice qu'elle cause sur diverses cultures à travers des dommages directs et comme vecteur de maladies virales. En Ouganda, les variétés de manioc utilisées ont succombé aux populations sans cesse croissantes de l'insecte occasionnant des dommages graves et des épidémies. Grâce à des interactions complexes avec la plante, le ravageur se nourrit en puisant dans le phloème de la plante et ce type de manœuvre sur la plante est réputé minimiser les réactions défensives des plantes. Un certain nombre de variétés de manioc ont montré de faibles populations du ravageur et des niveaux de dommages faibles sur le plan mondial. Bien que, plusieurs composants métabolites ont été retrouvés dans certaines variétés de manioc, les mécanismes de résistance du manioc face à *B. tabaci* ne sont pas encore bien compris. Les modifications

la teneur en métabolite par suite de l'interaction avec *B. tabaci* et leurs effets sur la résistance des cultures à l'insecte ne sont pas bien élucidés. Il est donc essentiel que des données scientifiques soient générées sur les métabolites présents au sein manioc pouvant être associés à la résistance à *B. tabaci* pour poser les bases d'amélioration des programmes de production de génotypes résistants de manioc. Cet article de synthèse présente un résumé concernant l'état de la recherche sur la résistance du manioc à *B. tabaci* et le développement de recherche en amélioration végétale des plant en Ouganda.

Key words: cassava, resistance mechanisms, secondary metabolites, *B. tabaci*, Uganda

Introduction

Cassava (*Manihot esculenta* Crantz) is an important and versatile crop grown in almost all parts of the world. It feeds both animals and an estimated 700 million people directly or indirectly in the world (Legg *et al.*, 2014). FAOSTAT (2016) provided an insight into the economic status of cassava where the statistics showed that cassava were grown on 20.7 million hectare of land worldwide and total production was 276.7 million tonnes in 2013. However, the yields worldwide stood at an estimated average of 15 ton/ha, while in Africa at 12.2 ton/ha and in Uganda at 13 ton/ha (FAOSTAT, 2016) compared to an optimum of 60-80 tons/ha (Howeler *et al.*, 2012). Yields are constrained as a result of abiotic stresses such as low soil nutrition, acidic soils and low rainfall (Nuwamanya, 2014). As regards the biotic stresses, cassava varieties used by farmers especially in Africa are prone to insect and viral attack (Chipeta *et al.*, 2015).

The whitefly (*Bemisia tabaci*) has been identified as a yield limiting factor which reduces yields by as high as 79% due to direct damage and as vector of disease (Howeler, 2012). Therefore minimizing the pest effect remains critical for cassava breeding and improvement programs (Legg *et al.*, 2014). Although cassava genotypes that support low whitefly populations have been identified, the interactions between the plant and the insect are not well understood (Bohorquez *et al.*, 2016). In as much as interactions between the host plant and phloem-feeding insects may change host plant suitability (Broekgaarden *et al.*, 2010) the internal characteristics of leaves, such as activity of plant defense-related enzymes in relation to the resistance mechanisms to *B. tabaci* have been less studied (Fürstenberg-Hägg *et al.*, 2013).

In this review we describe and discuss some recent aspects about cassava resistance to whitefly. In addition, we present cassava breeding initiatives in Africa and the recent development of cassava resistant to whitefly breeding strategy in Uganda.

Whitefly (*Bemisia tabaci*). The whitefly (*B. tabaci*) is classified under the Kingdom Animalia (Animals), Phylum Arthropoda (Arthropods), Subphylum Hexapoda (Hexapods), Class Insecta (Insects), Order Hemiptera (True Bugs, Cicadas, Hoppers, Aphids and Allies), Suborder Sternorrhyncha (Plant-parasitic Hemipterans), Super-family Aleyrodoidea, Family Aleyrodidae (Whiteflies), Genus Bemisia and Species tabaci (Brown, 1995).

Whiteflies generally feed and lay eggs on the under surfaces of young apical leaves. Estimated number of eggs lay per female range from 28 to 394 eggs (Byrne and Bellows, 1991). The eggs are pyriform or ovoid and have an extension of a chorion called pedicel. The pedicel is believed to be a guide for spermatozoa during fertilization (Byrne and Bellows, 1991) and also primary conduit through which water is absorbed from a plant (Buckner *et al.*, 2002). The eggs hatch to release crawlers (first instar) which possess functional legs able to move quickly in search of available minor veins and upon reaching the appropriate phloem they remain sessile till adult stage (Byrne and Bellows, 1991). The second and third instars resemble each other and differ in size (Legg, 1994) while the fourth instar or 'pupa' (Byrne and Bellows, 1991) is shield shaped, broadly elliptical (Gill, 1990) with two red eye spots at the anterior end visible beneath the translucent integument (Sseruwagi, 2005). Adult whiteflies after emergence from the pupa case differ in size with females being larger about 1mm and males about 0.8mm (Gill, 1990).

Bemisia tabaci has been identified as the most common out of 1, 500 whitefly species according to Anderson (2013). However, *B. tabaci* developmental time from egg to adult differs with the host plant it feeds on (Coudriet *et al.*, 1985). Twelve generations are attained annually under field condition on average (Legg, 1994). From the egg to the adult, developmental times were 107 days on cotton in India (Hussain and Trehan, 1933), 14.5 days on aubergine in Israel (Sseruwagi, 2005), 18.6 days on sweet potato, 29.8 days on carrot in the laboratory (Coudriet *et al.*, 1985). Newly emerged *B.tabaci* are sexually immature and copulation takes place 1 to 8h after emergence in summer (Byrne and Bellows, 1991). *B. tabaci* reproduce parthenogenetically with the unmated females producing only haploid male offspring while mated females producing both male and females. The ratio of male to female usually is 1:2 under field conditions and depends on host and host species, temperature and time of the year (Byrne and Bellows, 1991). On average, the longevity of the adults differs with females having longer life span (35 days) than the males (20 days) (Butler *et al.*, 1983).

Due to the difficulty faced in distinguishing different *B. tabaci* species morphologically, key biological features are employed to identify the different whitefly populations. *B. tabaci* have been known to exhibit distinct biological traits as in host-plant range and adaptability (Legg, 1994), inducement of plant physiological disorder (Costa and Brown, 1991) and plant virus transmission (Bedford *et al.*, 1994).

The whitefly causes damage to cassava plants through direct feeding, causing chlorosis of leaves (Perring *et al.*, 1991), stem blanching and reduction in plant vigour (Legg *et al.*, 2004). Heavy phloem feeding (Miller, 1990) leads to stunting of plants and yield loss, and indirectly, through the production of sticky sugary exudates or 'honey dew', which encourage development and growth of saprophytic fungi (e.g. *Capnodium* spp.) on the affected plants (Byrne *et al.*, 1990b). Induction of phytotoxic disorders results in silvering in some plants (Costa and Brown, 1991), which is restricted to a few genotypes (genetically distinct individuals for which formal taxonomic assignment has

not been determined) (Byrne *et al.*, 1995). These effects are especially severe when large populations of *B. tabaci* colonize plants.

B. tabaci is highly polyphagous (Asiimwe *et al.*, 2007) thus is not limited to just cassava but causes damage in tomato, cucumber, okra, beans and zucchini among other crops and this has hampered cultural as well as insecticide control strategies (Howeler, 2012). The ease of dispersion of the pest by wind (Navas-Castillo *et al.*, 2011) multiple breeding times in a year (multivoltine) and their rapid evolution (Anderson, 2013) has made bio control and insecticide use ineffective (Howeler, 2012).

In cassava research, although the damage is both direct and indirect, the indirect effects such as causing viral diseases have been focused on more than the direct components. Previously breeding work focused more on breeding resistant cassava varieties to CMD and CBSD, however, there is increased attention on breeding for whitefly resistant cassava varieties as the pest has been recognized as the underlying problem (Colvin *et al.*, 2015).

Breeding for cassava resistance to whitefly. Recent meetings and projects are trying to focus on the main issue, the whitefly, affecting most of the cassava varieties grown through breeding for resistance against *B. tabaci* (Colvin *et al.*, 2015). Since the 1990s, there has been an unprecedented increase in the abundance of cassava whitefly especially *B. tabaci* in cassava growing regions of East and Central Africa, which has in turn increased the spread of CMD and CBSD, though the factors responsible for increased whitefly abundance remain uncertain. In nine East and Central African countries production losses have been estimated as high as 47% and affected areas are continuing to expand, resulting in hunger, recurrent famines and annual losses of more than USD 1.25 billion (IITA, 2014). At the Global Cassava Partnership for the 21st Century (GCP21) meeting held in 2013 in Italy, breeding for whitefly resistance was one of the key actions (Legg *et al.*, 2014) where the development, implementation of effective whitefly management and multiplication of cassava cultivars resistant to all whiteflies was priority (Legg *et al.*, 2014). The International Whitefly Symposium (IWS), a series of specialized scientific meetings that resulted out of the merger of the International Bemisia Workshop (IBWS) and the European Whitefly Symposium (EWS) was held in Arusha, 2016. The focus was on best mitigating measures of the effects of the whitefly and stakeholders emphasized the importance of breeding varieties resistant to *B. tabaci* (CSIRO, 2016).

At the International Center for Tropical Agriculture (CIAT) in Colombia, more than 6000 cassava clones have been evaluated for resistance to whitefly *Aleurotrachelus socialis* (Caraballi *et al.*, 2012). In trials conducted in Ivory Coast with some 49 cassava varieties, field resistance was established to *B. tabaci* and offered potential for exploitation by breeders (Fauquet and Farguette, 1990). The South American variety MEcu 72 was identified as having resistance to *A. socialis* (Omongo *et al.*, 2012) and has been noted to be also resistant to *B. tabaci* (Bohorquez *et al.*, 2016). Another programme of research was carried out linking institutes in Africa, the UK and South America, to identify

possible resistance sources in cassava to the whitefly, *Bemisia tabaci*. The South American genotype M Ecu 72 and some Ugandan cassava landraces including Ofumba Chai, Nabwire 1 and Mercury showed good levels of resistance to *B. tabaci* (Omongo *et al.*, 2012). It is noted however, that there is minimal identified and documented evidence behind the cassava resistance to *B. tabaci*, and little is known about the resistance mechanisms (Bohorquez *et al.*, 2016).

Cassava leaves although reported to contain a lot of biochemical and anti-nutrient compounds (Achidi *et al.*, 2003) free sugars, protein and phenolic compounds (Koubala *et al.*, 2015) alkaloids, flavonoids and tannins (Anbuselvi and Balamurugan, 2014), their relation to *B. tabaci* resistance has not been studied. Many of these studies do not show the stage of growth of the cassava plants evaluated and were not conducted to observe the association of these compounds to *B. tabaci* resistance. There was no comparison of the metabolite content as regards resistant and susceptible genotypes of cassava to *B. tabaci*. The different levels of metabolite compounds throughout the growth period at different stages of growth (especially at peak *B. tabaci* infestation of the plant) for the crop have not been quantified. Moreover the effect the heritability of the genes controlling expression of these metabolite compounds has not been established as regards resistance to *B. tabaci*. There is therefore need to isolate and quantify the compounds in relation to cassava resistance to *B. tabaci*. For whitefly, it is clear that there is still a need for more knowledge on the biochemical changes that dictate the outcome of plant-insect interactions (Walling, 2008). Although vector infestation resulted in altered chemicals in the cassava leaves (Binu and Paliniswami, 2006), no information is available on how these changes influenced the resistance among the varieties.

For heritability studies, there is an information gap about cassava resistance to *B. tabaci*, making it difficult to make significant progress in breeding for resistance to *B. tabaci*. In contrast, resistance to arthropod pests have been documented more for example in the case of cassava mealy bug (CMB) and cassava green mite (CGM) (Ceballos *et al.*, 2015).

Cassava and *Bemisia tabaci* interactions. To date, little is known about cassava's resistance mechanism to whiteflies (Bohorquez *et al.*, 2016). Singh, (2009) strongly suggests that the ecological relationship between insects and plant tissues is a complex one with chemical interactions involved. Therefore understanding host plant interactions and the chemicals involved remains core in breeding for cassava resistance especially that it can increase plant resistance or decrease it (Broekgaarden *et al.*, 2007).

Whiteflies while on the leaf surface are exposed to chemicals, including secondary metabolites salicylic acid and jasmonic acid (SA/JA), which serve to attract or repel insects (Müller and Riederer, 2005). Some reports further have suggested that biochemical constituents such as peroxidases and phenolics in crops may contribute to whitefly resistance (Nombela and Muniz, 2010) as they affect fecundity, lead to malformed low nymph and adults and prolong development time (Ananthakrishnan, 1996).

Binu and Paliniswami (2006) conducted an evaluation on cassava in India on six week old cassava plants which were raised on a no choice test and infested with adult *B. tabaci*. During the study an evaluation of enzymes peroxidases, chitinase and the total protein content on resistant and susceptible varieties of cassava were made. The total protein content was determined using the protocol described by Bradford (1976) while enzyme activity was described following the protocol established by Abeles (1970). The total protein content in whitefly infested leaves decreased from 23.7mg/g to 21.94mg/g in resistant versus susceptible plants. Total as well as specific activities of enzymes were higher in whitefly infested leaves. In another evaluation total protein content in cassava varieties resistant (MEcu 64, MEcu 72 and MPer 334) to *A. socialis* against a susceptible check was conducted using electrophoresis on Polyacrylamide gels (PAGE). According to CIAT (2004) the differences shown between the resistant and susceptible genotypes were a good indication that a relationship existed between protein and the presence of resistance to *A. socialis*. In Uganda, research carried out by Omongo *et al.* (2012) where an assessment of the South American whitefly-resistant germplasm from the neotropics against African cassava *B. tabaci* was done. The work identified some Ugandan landraces with low populations of *B. tabaci* and determined that there were no obvious correlations between plant traits such as “bitter or sweet” and resistance to *B. tabaci*.

Way forward

Since resistance can be monitored by the interaction of several metabolic pathways (Meihls *et al.*, 2012) quantification of the various biochemical components that are present in the cassava plant with different resistance levels and during different stages of growth is necessary. Such findings could be used to further study the metabolic interaction and expression patterns of the different cassava pest defense pathways (Barah and Bones, 2015). The study of the different quantities of secondary metabolites such as SA, alkaloids and flavonoids, protein and enzymes in cassava would be able to show the interaction of various pathways leading to these compounds and further, their priming effects (Ahmed, 2012). This would also improve selection of varieties that are resistant to *B. tabaci*. The study of the mode of inheritance of the genes controlling the metabolites closely associated with cassava resistance to *B. tabaci* would enhance the efficiency and efficacy of breeding resistant cultivars to *B. tabaci*.

Since no secondary metabolite (SA, peroxidase, flavonoids, alkaloids, tannins) and protein content investigation has been carried out on Ugandan varieties, it is important to quantify the metabolites on Ugandan varieties and evaluate changes at different times during the *B. tabaci* attack. This will strengthen the understanding of the biochemical and molecular basis of cassava resistance to *B. tabaci*.

The identification of metabolites such as SA, peroxidase and tannins in relation to *B. tabaci* resistance can lead to gene expression analysis, construction of genetic maps, and genome sequence analysis (Nombela and Muniz, 2010).

At the moment, NRI, NaCRRI, CIAT, Makerere University and other research organizations in the Great Lakes region are currently undertaking research to this effect. In this respect, a study focused towards identifying the secondary metabolites and the mode of inheritance of the genes controlling these compounds in some Ugandan local and improved cultivars will provide useful information that can be used to further breeding work in cassava resistant to *B. tabaci*.

Acknowledgements

The authors thank DAAD and Carnegie Corporation of New York, USA for financing this study. Gratitude is also extended to the Regional Universities Forum for Capacity Building in Agriculture (RUFORUM), National Crops Resources Research Institute (NaCRRI), Namulonge, Uganda, Makerere University, Uganda and University of Zambia, for various forms of support. This paper is a contribution to the 2016 Fifth African Higher Education Week and RUFORUM Biennial Conference.

References

- Achidi, A. U., Ajayi, O. A., Maziya, D. B. and Bokanga, M. 2008. The effect of processing on the nutrient content of cassava leaves. *J. Food. Process. Preserv.* 32 (3):486-502.
- Ananthakrishnan, 1996. National symposium on biochemical bases of host plant resistance to insects. Proceedings, National Academy of Agricultural Sciences, New Delhi, India.
- Anbuselvi, S. and Balamurugan, T. 2014. Phytochemical and anti-nutrient constituents of cassava and sweet potato. *World Journal of Pharmacy and Pharmaceutical Sciences* 3(3): 1440-1449.
- Anderson, 2013. Control Strategies for Whitefly as a Vector for Cassava Viral Diseases. EPAR Brief No. 233.
- Asiimwe, P., Ecaat, J. S., Otim, M., Gerling, D., Guershon, M., Kyamanywa, S. and Legg, J. P. 2007. Life table analysis of mortality factors affecting populations of *Bemisia tabaci* on cassava in Uganda. *Entomologia experimentalis et applicata* 122 (1): 37-44.
- Bedford, I. D., Briddon, R. W., Brown, J. K., Rosell, R. C. and Markham, P. G. 1994. Geminivirus transmission and biological characterisation of *Bemisia tabaci* (Gennadius) biotypes from different geographic regions. *Annals of Applied Biology* 125 (2): 311–325. <http://doi.org/10.1111/j.1744-7348.1994.tb04972.x>
- Binu, A. and Palaniswami, A. M. 2006. Bemisia feeding induces pathogenesis related proteins in cassava (*Manihot esculenta* Crantz). *Indian Journal of Biochemistry and Biophysics* 43 (3): 182-185.

- Bohorquez, A., Lopez-Lavalle, B., Bellotti, A. and Tohme, J. 2016. Unraveling whitefly resistance in cassava. CIAT Agrobiodiversity and Biotechnology Project, AA6713.
- Broekgaarden, C., Poelman, E.H., Steenhuis, G.M, Voorrips, R. E., Dicke, M. and Vosman, B. 2007. Genotypic variation in genome-wide transcription profiles induced by insect feeding: *Brassica oleracea*-*Pieris rapae* interactions. *BMC Genomics* 8:239.
- Broekgaarden, C., Pelgrom, K. T. B., Voorrips, R.E., Bas, N., Visser, R. G. F. and Vosman, B. 2014. Host plant resistance towards the cabbage whitefly in *Brassica oleracea* and its wild relatives. *Euphytica* 202(2): 297-306.
- Brown, J. K., Coats, S. A., Bedford, I. D., Markham, P. G., Bird, J. and Frohlich, D. R. 1995. Characterization and distribution of esterase electromorphs in the whitefly, *Bemisia tabaci* (Genn.) (Homoptera: Aleyrodidae). *Biochemical Genetics* 33 (7-8): 205–214.
- Brown, J. K., Frohlich, D. R., and Rosell, R. C. 1995. The sweetpotato or silverleaf whiteflies: Biotypes of *Bemisia tabaci* or Species Complex. *Annual Review of Entomology* (40): 511–534.
- Butler Jr., G. D., Henneberry, T. J. and Clayton, T. E. 1983. Development of *Bemisia tabaci* (Homoptera: Aleyrodidae) in relation to temperature. *Annals of the Entomological Society of America* 76 (2): 310–313.
- Butler, N.S., Vir, B. K., Kaur, G., Singh, T. H. and Raheja, R. K. 1992. Biochemical basis of resistance to whitefly *Bemisia tabaci* Genn. (Aleyrodidae: Hemiptera) in cotton. *Trop. Agric. (Trinidad)*. 69 (2);119-122.
- Byrne, D. N. and Bellows, T. S. J. 1991. Whitefly biology. *Annual Review of Entomology* 36 (81): 431–457.
- Carabalí, A., Belloti, A. C. and Montoya-Lerma, J. 2012. Biological parameters of *Bemisia tabaci* (*Gennadius*) biotype B (*Hemiptera: Aleyrodidae*) on *Jatropha gossypifolia*, commercial (*Manihot esculenta*) and wild cassava (*Manihot flabellifolia* and *M. carthaginensis*) (*Euphorbiaceae*). *Neotropical Entomology* 39 (4): 562-567.
- Ceballos H., Kawuki, R. S., Gracen, V. E., Yecho, G. C. and Hershey, C. H. 2015. Conventional breeding, marker-assisted selection, genomic selection and inbreeding in clonally propagated crops: a case study for cassava. *Theor Appl Genet* 128: 1647-1667 DOI 10.1007/s00122-015-2555-4.
- Chipeta, M. M., Bokosi, J. M. and Saka, V. W. 2015. Genetic analysis in a six parent diallel cross of cassava (*Manihot esculenta* Crantz). *African Journal of Agricultural Research* 10 (10): 1076–1082. <http://doi.org/10.5897/AJAR2014.9067>.
- Colvin, J., Omongo, C. A., Maruthi, M. N., Otim-Nape, G. W. and Thresh, J. M. 2004. Dual begomovirus infections and high *Bemisia tabaci* populations: Two factors driving the spread of a cassava mosaic disease pandemic. *Plant Pathology* 53 (5): 577–584. <http://doi.org/10.1111/j.1365-3059.2004.01062.x>
- Costa, H. S., and Brown, J. K. 1991. Variation in biological characteristics and esterase patterns among populations of *Bemisia tabaci*, and the association of one population with silverleaf symptom induction. *Insect Science* 61 (3): 211–219.
- Coudriet, D. L., Prabhaker, N., Kishaba, A. N. and Meyerdirk, D. E. 1985. Variation

- in developmental rate on different hosts and overwintering of the sweetpotato whitefly *Bemisia tabaci* (Homoptera: Alleyrodidae). *Environmental Entomology* 14 (4): 516–519.
- CIAT (Centro Internacional de Agricultura Tropical), 2003. Annual report 2003 Project IP3:
- Fauquet, C. and Fargette, D. 1990. African Cassava Mosaic Virus: Etiology, Epidemiology, and Control. *Plant Disease* 74 (6): 404-411.
- FAOSTAT, 2016. Crop production updates. Retrieved 10th June from <http://faostat.fao.org/site/339/default.aspx>.2016.
- Fürstenberg-Hägg, J., Zagrobelny, M. and Bak, S. 2013. Plant defense against insect herbivores. *International Journal of Molecular Science* 14:10242-10297.
- Gill, R. J. 1990. The Morphology of Whiteflies. Gerling, D. (Ed.), Whiteflies Their Bionomics Pest Status and Management. Intercept.
- Hussain, M. A. and Trehan, K. N. 1933. Observations on the life-history, bionomics and control of the white-fly of cotton (*Bemisia gossypiperda* M. and L.). *Indian J Agric Sci.* 3 (4): 701–753.
- Howeler, R. H. (Ed.). 2012 The cassava handbook: A reference manual based on improved cassava for the developing world. CIAT, Cali, Colombia.
- International Institute of Tropical Agriculture (IITA), 2001. Research guide 55. Physiol. Cassava. Cassava Plant. 3rd Nov. (<http://www.iita.org/info/tm-mat/irgss/irg553.html>). p.2.
- Koubala, B. B., Miafo, A.P.T., Bouba, B., Kamda, A.G. S. and Kansci, G. 2015. Evaluation of insecticide properties of ethanolic extract from *Balanites Aegyptiaca*, *Melia azedarach* and *Ocimum gratissimum* leaves on *Callosobruchus maculatus* (Coleoptera: Bruchidae). *Asian Journal of Agricultural Sciences* 5 (5): 93-101.
- Legg, J. 1994. *Bemisia tabaci*: The whitefly vector of cassava mosaic Gemini viruses in Africa: An ecological perspective. *African Crop Science Journal* 2(4): 437-448.
- Legg, J. P., Sseruwagi, P., Boniface, S., Okao-Okuja, G., Shirima, R., Bigirimana, S., Gashaka, G., Herrmann, H-W., Jeremiah, S. C., Obiero, H. M., Ndyetabula, I., Tata-Hangy, W., Masembe, C. and Brown, J. K. 2013. Spatio-temporal patterns of genetic change amongst populations of cassava *Bemisia tabaci* whiteflies driving virus pandemics in East and Central Africa. *Virus Research* 186 : 61-75.
- Legg, J. P. and Fauquet, C. M. 2004. Cassava viruses in Africa. *Plant Mol Biol* 56: 585–599.
- Legg, J., Shirima, R., Tajebe, L., Guastella, D., Boni, S. and Jeremiah, S. C. 2014. Biology and management of Bemisia whitefly vectors of cassava virus pandemics in Africa (PDF Download Available). Available from: https://www.researchgate.net/publication/261411032_Biology_and_management_of_Bemisia_whitefly_vectors_of_cassava_virus_pandemics_in_Africa [accessed May 5, 2016].
- Müller, C. and Riederer, M. 2005. Plant surface properties in chemical ecology. *J Chem Ecol* 31: 2621–2651.
- Nombela, G. and Muniz, M. 2010. Host plant resistance for the management of *Bemisia tabaci*: A multi crop survey with emphasis on tomato. Binomics and management of a global pest. pp. 357-383.

- Navas-Castillo, J., Fiallo-Olivé, E. and Sánchez-Campos, S. 2011. Emerging virus diseases transmitted by whiteflies. *Annual review of phytopathology* 49: 219-248.
- Nuwamanya, E., Rubaihayo, P., Mukasa, S., Kyamanywa, S., Hawumba, J. and Baguma, Y. 2014. Biochemical and secondary metabolites changes under moisture and temperature stress in cassava (*Manihot esculenta* Crantz). *African Journal of Biotechnology* 13 (31):3173-3186.
- Omongo, C. A., Kawuki, R. S., Bellotti, A. C., Alicai, T., Baguma, Y., Maruthi, M. N. and Colvin, J. 2012. African Cassava Whitefly, *Bemisia tabaci*, resistance in African and South American cassava genotypes. *Journal of Integrative Agriculture* 11(2): 327-336.
- Colvin, J., Seal, S. and Summers, G. 2015. NRI awarded major grant to tackle cassava whitefly in Sub-Saharan Africa. <http://www.nri.org./news/2015>.
- Perring, T. 2001. The *Bemisia tabaci* species complex. *Crop Protection* 20 (9): 725–737. [http://doi.org/10.1016/S0261-2194\(01\)00109-0](http://doi.org/10.1016/S0261-2194(01)00109-0).
- Sseruwagi, P., Legg, J. P., Maruthi M. N., Colvin J., Rey M. E. C. and Brown, J. K. 2005. Genetic diversity of *Bemisia tabaci* (*Gennadius*) (*Hemiptera:Aleyrodidae*) populations and presence of the B. biotype and a non-B biotype that can induce silverleaf symptoms in squash, in Uganda. *Entomol Exp Applic* 122: 37–44.
- Walling L. L. 2008. Avoiding effective defenses: Strategies employed by phloem-feeding insects. Department of Botany and Plant Sciences, Center for Plant Cell Biology, University of California, Riverside, California 92521–0124.