Journal of Agriculture and Ecology Research International

17(2): 1-18, 2018; Article no.JAERI.47706
ISSN: 2394-1073

Genetic Variability for Flowering Time, Maturity and Drought Tolerance in Cowpea [*Vigna unguiculata* (L.) Walp.]: A Review Paper

M. S. Alidu[1*]

[1]*Department of Agronomy, Faculty of Agriculture, University for Development Studies, P.O.Box TL 1882, Nyankpala, Tamale, Ghana.*

Author's contribution

The sole author designed, analysed, interpreted and prepared the manuscript.

Article Information

DOI: 10.9734/JAERI/2018/v17i230044
Editor(s):
(1) Dr. Nhamo Nhamo, Associate Professor,Marondera University of Agricultural Sciences and Technology, Marondera, Zimbabwe.
Reviewers:
(1) Toungos, Mohammed Dahiru, Adamawa State University Mubi, Nigeria.
(2) Jamile Da Silva Oliveira, EMBRAPA, Brasil.
Complete Peer review History: http://www.sdiarticle3.com/review-history/47706

Review Article

Received 15 December 2018
Accepted 22 February 2019
Published 15 March 2019

ABSTRACT

Background: Cowpea plays a critical role in the lives of millions of people in Africa and other parts of the developing world, where it is a major source of dietary protein that nutritionally complements staple low-protein cereal and tuber crops. It is a valuable and dependable commodity that produces income for farmers and traders. Objective: To review related research work on the genetic variability for time to flowering, maturity and drought tolerance in cowpea.

Data Source: Searches were made from the following databases and archives; International Institute of Tropical Agriculture (IITA), The Essential Electronic Agricultural Library (TEAL), Access to Global Online Research in Agriculture (AGORA) (FAO), AGRICOLA (National Agricultural Library), AGRIS - Agricultural Sciences and Technology (FAO), CAS - Chemical Abstracts (ACS), DOAJ - Directory of Open Access Journals, CABI, Euphytica, Elsevier, Research Alert, Scopus and CGIAR, Plant Genetics and Breeding Database, Crop Science Database, Plant Genetics and Breeding Database, data base repositories, using the terms "genetic variability", "drought", "tolerance", " time to flowering and maturity", and "cowpea" individually or in combination to identify literature published in English language between January 1990 to January 2018.

Methods: The review was carried out using the above search terms. Research papers were critically reviewed, relevant data extracted, and a narrative synthesis was conducted to determine the relevant papers.

**Corresponding author: E-mail: msanatu@uds.edu.gh;*

Results: In all 150 papers met the inclusion criteria. Collections were from varied background; Sub-Saharan Africa, Asia, Europe, and Latin Americas.
Conclusion: Despite research studies on cowpea and drought, there appears to be limited such research findings on the time to flowering, and maturity in relations to drought tolerance in cowpea in Ghana, suggesting more research in this part of the world.

Keywords: Vigna unguiculata (L.) Walp.; drought; phenology; markers and participatory rural appraisal.

1. INTRODUCTION

Cowpea plays a critical role in the lives of millions of people in Africa and other parts of the developing world, where it is a major source of dietary protein that nutritionally complements staple low-protein cereal and tuber crops, and is a valuable and dependable commodity that produces income for farmers and traders [1–3]. The drier Savanna and the Sahelian region of West and Central Africa produce about 70% of worldwide cowpea production, with Nigeria, Niger and Brazil being the largest producers.

Cowpea is called “poor man’s meat”, because the seed protein contents range from 23% to 32% of seed weight rich in lysine and tryptophan, and a substantial amount of mineral and vitamins (folic acid and vitamin B) necessary for preventing birth defect during the pregnancy stage [4]. Also, plant food diets such as cowpea increase the level of fibre intake which reduces the risk of bowel diseases, including cancer and also reduction in osteoporosis incidence [5]. The cooking liquor of the seeds with spices is considered to be a potential remedy for the common cold. Leaves are boiled, drained, sun-dried and then stored for later use. Zia-Ul-Haq [6] reported that, Seed oil exhibit antidiabetic properties, Seeds also possess nematicidal and antifungal properties.

In many parts of West Africa, cowpea hay is also critical in the feeding of animals during the dry season, in addition, cowpea is a nitrogen-fixing plant, when used in rotation with cereal crops it can help restore soil fertility. Therefore, cowpea can play an important role in the development of agriculture [7].

2. ORIGIN, DOMESTICATION AND TAXONOMY OF COWPEA

The name cowpea probably originated from the fact that the plant was an important source of hay for cows in the south-eastern United States and in other parts of the world [1]. Speculations on the origin and domestication of cowpea [*Vigna unguiculata* (L.) Walp.] have been based on botanical and cytological evidence, information on its geographical distribution as well as cultural practices and historical records [8].

Huynh et al. [9] reported that cowpea first moved from West Africa to the World with African people during the slave-trading period. However, no documentation occurred to support the extent of the movement. Other researchers also believe that cowpea originated from West Africa, although the exact location of the centre of origin of the species is not known. Huynh et al. [9] used SNP makers to study the gene pool structure of African wild annual cowpea *V. unguiculata* subsp. *dekindtiana* from both East and West Africa and to determine their kinship or how they are related to African wild cowpeas and non-African domesticated cowpeas. These authors found that out the genetic materials diverged into two gene pools. In a related study, Batieno [10] reported that, the two gene pools were distributed in two distinct geographical zones separated by the dense and vast rainforests of the Congo River basin. In a related study, cowpea remains were discovered from Kintampo in Ghana and carbon dated to about 1400 - 1480 BC making it the oldest archaeological evidence of the crop [11].

A study which also utilized over 10,000 accessions of world collection at the International Institute of Tropical Agriculture (IITA) discovered that the collection from West Africa spread to India by 2000 BC [12]. It was introduced into Europe by the Greeks and Romans who grew it under the name Phaseolus. It was introduced into the Americas relatively more recently. The research work carried out by IITA showed that germplasm accessions from West Africa showed greater diversity than those from East Africa [12]. These studies provided further evidence that West Africa was the primary centre of domestication. The centre of maximum diversity of cultivated cowpea is found in West Africa, encompassing the Savanna regions of Nigeria, southern Benin, Togo, and north-west part of

Cameroon [8]. Verdcourt [13] reported that Vigna has several species, but the exact number varies according to different authors.

The cultivated cowpea is grouped under subspecies *unguiculata,* which is further subdivided into four cultivar groups namely; *unguiculate* which is the common form; biflora or *catjang* which is characterised by small erect pods and found mostly in Asia, and *sesquipedalis,* or yard-long bean, also found in Asia and characterised by its very long pods which are consumed as green 'bean'; and *textilis*, found in West Africa and which was used for fibre obtained from its long peduncles [8].

The cultivar group *unguiculata* is the most diverse of the four and is widely grown in Africa, Asia and Latin America [14]. Subspecies *unguiculata* is the only cultivated cowpea, while the other three are wild relatives. Several studies have shown that cowpea was probably domesticated by African farmers [15] and assumed to have evolved in Africa, because wild cowpeas only exist in Africa and Madagascar [16]. Although the centre of diversity of wild Vigna species is in south-eastern Africa, West Africa is a major centre of diversity of cultivated cowpea [12]. Coulibaly and Lowenberg-De Boer [17] used data from amplified fragment length polymorphism (AFLP) marker analyses of cowpea accessions to hypothesize that cowpea domestication occurred in north-eastern Africa and could have occurred at the same time with the domestication of sorghum and pearl millet in the third millennium B.C. [16].

Evolution processes of *V. unguiculata* resulted in a change in growth habit, that is, from perennial to an annual breeding crop and from predominantly out-breeding to inbreeding. The cultivated cowpea evolved through domestication and selection [12].

Huynh et al. [9] reported that cowpea is a diploid crop with 11 pairs of chromosomes (2n = 2x = 22) and 630 Mb genome size. Cowpea is a *Dycotyledonea* belonging to order *Fabales*, family *Fabaceae*, subtribe *Phaseolinae*, genus *Vigna,* and section *catiang* [18,8]. The subspecies include: *unguiculata, stenophylla*, *dekindtiana* and *tenuis* [8].

3. PLANT CHARACTERISTICS

The plant is herbaceous and may be erect, prostate or twinning. The flowers may be purple, yellow, pink or blue. The pods may be black, purple or cream when dry and hang downwards, pointing upwards or sideways. Pod length of up to 60 cm has been recorded [19]. Seeds may be white, cream, purple, red, and brown, mottle brown or black in colour. Four types of grain coat texture have been identified in cowpea: smooth, rough, wrinkled and loose [20]. Preference for grain coat texture differs across various parts of the world. For instance, cowpeas with large white or brown grains with rough grain coat are preferred throughout West Africa, whereas in East Africa they prefer medium size, brown or red grains with smooth grain coat. In some Latin American countries, principally Cuba and part of Caribbean, black colour with various categories of grain coat texture are preferred [21]. In West and Central Africa, rough grain coat is preferred since it permits easy removal of the grain coat which is essential for indigenous food preparations [22]. Umar [23] reported that the preference for cowpea grain with rough grain coat in Nigeria is due to their ease of dehulling and greater expansion capacity. Grain coat colour is also considered as one of the useful phenotypic markers in cowpea breeding due to its stable expression and suitability for observation [24].

4. COWPEA PRODUCTION AND DISTRIBUTION

Cowpea is cultivated throughout the African continent as well as in some parts of South East Asia and Latin America. Though native to West Africa, this legume has become a part of the diet of about 110 million people [25]. In West Africa, cowpea has become an integral part of the farming systems [25]. Cowpea production in the world was estimated at 12.5 million hectares, with an annual output of more than 3 million tons [26]. Africa alone produces about 83% of the world output. Nigeria is the largest world's producer (45.76%), followed by Niger (15%), Brazil (12%), and 5 % for Burkina Faso [27], with Africa's arid Sahel region accounting for 64%. In Ghana, cowpea cultivation is primarily done in the northern and upper West regions. Cowpea commercial regions include the Upper East, Brong Ahafo, Eastern, Volta and Ashanti. The Ghana government policy objective for the cowpea subsector is to encourage increased production so that self-reliance and food security can be achieved. Yet, the production of the crop has fluctuated over the years partly due to climatic conditions and policy issues [28]. Average yield of cowpea in Ghana is 1,3 t/ha with a potential estimated at 1.96 t/ha [29].

Cowpea farming serves as a vital component of sustainable cropping system in Ghana because of its nitrogen fixing ability and socio-cultural values [30]. The crop is considered drought and heat tolerant, and is able to fix nitrogen up to 240 t/ha and leaving about 60–70 kg nitrogen for the following crops [31]. Production is mainly done by small-scale resource-poor farmers practicing mostly peasant agriculture and growing largely unimproved varieties resulting in low output. SARI [32] carried out studies, which showed an adoption rate per annum of 3.9% for improved varieties in northern Ghana, confirming that majority of farmers still grow landraces or unimproved varieties of the crop.

4.1 Climate and Soil Requirements for Cowpea Production

Cowpea is predominantly a hot weather crop grown in many parts of the tropical world [33]. It thrives well between the temperature ranges of 20-35°C, since temperature above 35°C, is known to reduce yield. Heat stress is often defined as a situation where temperatures are high enough for sufficient period that can cause irreparable dam [34,35] age to the plant function or development which shortens the time for photosynthesis to contribute to seed production [36]. Comparison of cowpea growth and grain yield under tropical and subtropical conditions have shown that high temperature is an important stress factor for cowpea [36,37]. Many stages of the crop are sensitive to high temperature [38,39]. In general, higher temperatures shorten the period of reproductive growth, and grain yield is consequently reduced. In addition to warmer temperatures accelerating crop development, high temperatures also allow little time for carbon assimilation that could be partitioned to the grain and substantially reduces yield [40]. Singh [41] reported that flower and pod shedding also increase at temperatures above 35°C leading to a marked reduction in yield. Cowpea requires a rainfall of 600 to 800 mm per annum for optimum growth and development. Medium and long duration types require a rainfall between 600 and 1500 mm per annum [42]. Excessive rain or atmospheric humidity results in reduction in yield due to a high incidence of fungal diseases [43].

High night temperatures appear to be more damaging than high day temperatures [44]. High night temperatures can cause male sterility in cowpea [45]. The stage of floral bud development most sensitive to high temperatures occurs seven to nine days before anthesis, that is after meiosis, and involves premature degeneration of tapetal tissue and lack of endothelial development [46]. Transport of proline from anther walls to pollen is therefore inhibited in sensitive genotypes [47].

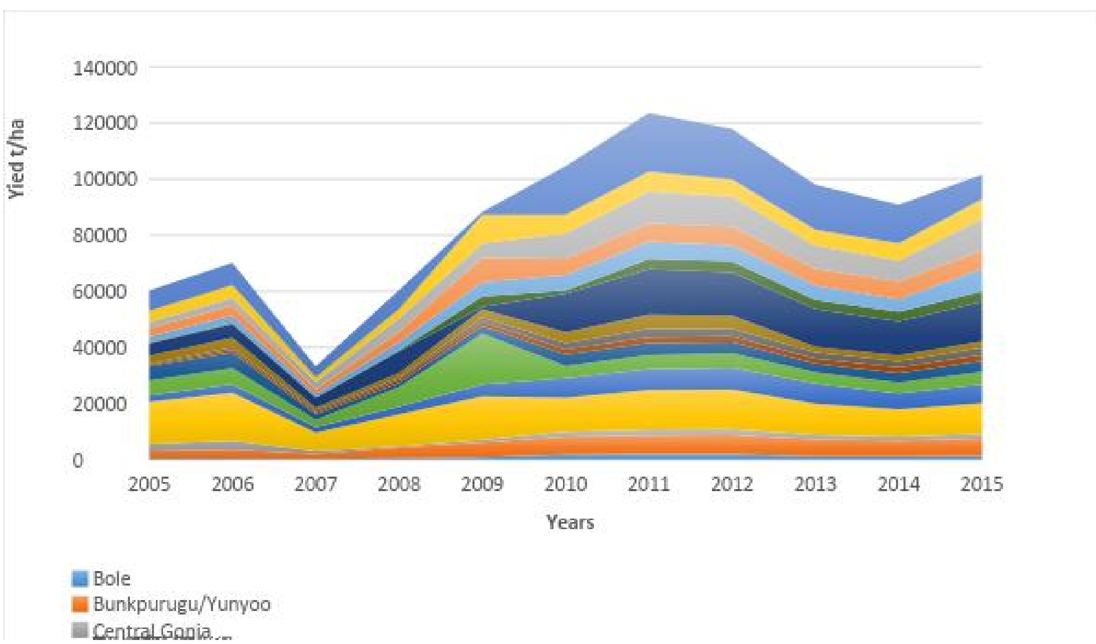

Fig. 1. A graph showing trend of cowpea production in Northern Ghana- (MOFA-SRID, 2016)

Cowpea is sensitive to photoperiod; thus, short day, day neutral and long-day types of cowpea exist [48]. Cowpea responses to photoperiod determine the time of first flowering and the length and effectiveness of the reproductive period [49].

Some cultivars have a quantitative response to photoperiod such that flowering is delayed by long days, while others are day-neutral in that the initiation of floral bud is not influenced by day length [38]. However, plant breeders have successful in the development of photoperiod sensitive cultivars [50].

Cowpea grows well over a range of soils, from sands to heavy expandable clays but well drained soil is most preferred, as the crop cannot tolerate water logging [51]. Cowpea can be inter-cropped with maize, millet, sorghum, cassava or even rice in the traditional farming systems of the tropics. In such intercropping systems cowpea is often subjected to zero tillage practices developed mainly for the companion crop [52].

4.2 Effects of Moisture Stress on Cowpea and Genetic Variation in Drought Tolerance

The effects of moisture stress on plant physiology differ with species and degree of tolerance as well as with the extent of the water deficit. Generally, moisture stress affects the process related to cell turgidity and particularly meristematic growth. If moisture stress continues, other physiological processes are affected. For instance, moisture stress changes stomatal opening leading to a reduction in photosynthetic rates and water transport through the xylem. This in turn causes reduced transport flux of absorbed nutrients by roots and in the whole plant [53]. This impedes phenological development leading to marked reduction in yield.

Several physiological processes, including osmotic adjustment and desiccation tolerance, have been suggested as contributing to adaptation to drought. Cowpea, however has displayed little osmotic adjustment in leaves [54]. Some genotypic differences have been reported in the ability of cowpea to survive imposed drought start of vegetative growth [55]. The ability of cowpea to survive vegetative stage drought is related to the sensitive responses of their stomata to soil water deficit [56] and maintenance of high leaf water potentials [57]. Studies have been conducted in which cowpea was subjected to drought during the vegetative stage and the reproductive stage, which showed that grain yield of cowpea is strongly dependent upon the water supply during the reproductive stage, with relatively little effect at the vegetative phase [57,58]. However, further related studies have also shown that drought stress at the flowering or pod filling stages causes senescence and abscission of mature basal leaves. Akyeampong [59] and Gwathmey and Hall [60] reported that determinate cowpea that begins flowering early, but have delayed leaf senescence are able to recover after mid-season drought probably resulting from the maintenance of root viability, which could also enhance nitrogen fixation.

Early maturing varieties escape terminal drought [42] but if exposed to intermittent moisture stress during the vegetative growth stage, they perform very poorly [61]. Reductions in leaf area are responsible for drought induced reductions in seed yield of cowpea [62]. Summerfield and Roberts [63] and Minchin and Summerfield [64] have argued that early maturity varieties depend more on drought escape mechanisms, which enables them to complete their life cycle before the incidence of terminal drought. If, however, they are exposed to erratic moisture stress during the vegetative or reproductive stages, they perform very poorly. Many aspects of plant growth are affected by drought stress [65], including leaf expansion, which is reduced due to the sensitivity of cell growth to water stress. Water stress also affects total leaf production, promotes senescence and abscission [66] resulting in decreased total leaf area per plant. Reduction in leaf area reduces crop growth and thus biomass production and seed yield is affected [59].

4.3 Vegetative Growth and Water Stress

The vegetative part of the plant is made up of two main components: The mature leaves that function as a source of assimilates and the expanding leaves that act as a sink of assimilates in competition with reproductive organs and roots. In legumes, Ney and Wery [67] hypothesized that, in the absence of drought or heat stress, assimilates are specially translocated to vegetative sinks, thereby inducing abortion of flowers, until a sufficient amount of seeds reach the seed-filling stage. Seed growth then becomes the central sink and stimulates the terminate leaf appearance and abortion of the youngest seeds on the top of the plant [68]. Expanding leaves show a large range of size and age, from the last phytomer produced by the apical meristem of a shoot to the first visible leaf out of the apical bud.

Comprehensive descriptions of leaf and phytomer development were made in contrasting species for a large range of growing conditions including pea [69] cotton [70], white clover [71], and grapes [72]. An extended or more intense water deficit is required to obtain a significant reduction of vegetative sources because these same 10 leaves will become sources after a time-span of 10 phytochromes and may even not be all expanded if vegetative growth is stopped by reproductive sinks. For this reason and also because expanding leaves make a minor contribution to light interception compared with expanded leaves, the vegetative sources (represented, for example, by leaf area index) are given a lower sensitivity to water deficit than vegetative sinks. This effect has been detected in annual plants such as chickpea, cowpea, and cotton, it is more distinct in perennial plants such as white clover and vineyards [72,73]. Among the processes involved in plant leaf area expansion, branching and leaf appearance on the main stem, the most and the least sensitive processes to water deficit, leaf expansion have an intermediate response to water stress [74].

4.4 Variation in Days to Flowering, Maturity and Yield in Cowpea

One of the important agronomic traits in cowpea production is earliness which is measured by days to flowering and days to maturity. Many quantitative studies on the genetics of earliness parameters have showed high heritability estimates of 0.75 for days to flowering and 0.79 for days to pod maturity [75]. Hall and Patel [76] reported that early erect cowpea cultivars, which commence flowering about 30 days after sowing in the tropics, have proved to be useful in some dry environments because of their ability to escape drought. Also, Wien [77] reported that, the longer the reproductive period the larger the number of fruits that mature and the larger the yield. Genetic differences in the period of the reproductive period is related to growth habit.

4.5 Drought Tolerance Mechanisms in Cowpea

Traditionally drought tolerance is defined as the ability of plants to live, grow and yield satisfactorily with limited soil water supply or under periodic water deficiencies [78]. Plants have established a number of elaborate molecular mechanisms to respond and adapt to various environmental stresses, including drought and high temperatures [79]. Batieno *et al.* [80] indicated that drought occurrence can be sporadic in the life cycle of crop plants. Bahar and Yildirim [81], also reported that, crops are highly vulnerable to damage due to limited water during flowering and pod setting stages. Selection of drought tolerant lines has been based on one of the mechanisms such as avoidance so that early maturing lines used as escape would have completed physiological maturity before the incidence of drought [10]. Studies on genetic variability and diversity in drought tolerance has been conducted to assist in the identification of suitable parents to improve cowpea for drought tolerance [82].

Numerous factors and mechanisms operate independently or jointly to enable plants cope with drought stress. Therefore, drought tolerance is manifested as a complex trait [83]. According to Mitra [84], the mechanisms that plants use to survive drought stress can be grouped into three categories. These include drought escape, drought avoidance and drought tolerance. Drought escape is defined as the ability of a plant to complete its life cycle before serious soil and plant water deficits occur. Drought avoidance is the ability of plants to sustain relatively high tissue water potential despite a shortage of soil moisture. Drought tolerance is the ability of plants to withstand water-deficit with low tissue water potential [20].

Crop plants therefore use more than one mechanism at a time to cope with drought. These mechanisms involve rapid phenological development (early flowering and early maturing), developmental plasticity (variation in duration of growth period depending on the extent of water deficit) and remobilization of pre-anthesis assimilates. Plants develop strategies for maintaining turgor by increasing root depth or developing an efficient root system to maximize water uptake, and by reducing water loss through reduced epidermal, stomatal and lenticular conductance, reduced absorption of radiation by leaf rolling or folding and reduced evapo-transpiration surface [84]. According to Agbicodo et al. [85], the mechanisms of drought tolerance in cowpea are maintenance of turgor through osmotic adjustment (accumulation of solute in cell), increased cell elasticity and decreased cell size and desiccation tolerance by protoplast resistance. However, all these adaptation mechanisms of the plant to cope with drought have some disadvantages with respect to yield potential. For instance, a genotype with a shortened life cycle (drought escape) usually yields less compared to a genotype with a normal life cycle.

The mechanisms that confer drought avoidance act by reducing water loss (such as stomatal closure and reduced leaf area) decrease carbon assimilation due to a reduction in physical transfer of carbon dioxide molecules, and increase leaf temperature thus reducing biochemical processes, which negatively affects yield. Plants try to maintain water content by accumulating various solutes that are nontoxic (such as frutans, trahalose, glycines betane, proline and polyamines) and do not interfere with plant processes and that are, therefore called compatible solutes [86]. However, many ions concentrated in the cytoplasm due to water loss are toxic to plants at high concentrations leading to what is termed a glassy state.

In this condition, whatever liquid is left in the cell has a high viscosity, increasing the chances of molecular interactions that can cause proteins to denature and membranes to fuse [87]. Subsequently, crop adaption to water stress must reflect a balance among escape, avoidance and tolerance while maintaining adequate productivity. Though drought escape, avoidance, and tolerance mechanisms have been described in cowpea [84], the drought response pathways associated with these mechanisms are not yet fully understood, and the degree to which these operate together or separately to allow the crop to cope with drought still needs to be established.

4.6 Drought Escape in Cowpea

The increased frequency of drought in some cowpea growing areas caused a shift to early maturing varieties [88]. Early maturing cowpea cultivars are desirable and have proven to be useful in some dry environments and years because of their ability to escape drought [75,89]. Such early cultivars can reach maturity in as few as 60-70 days in many of the cowpea production zones of Africa. Earliness is important in Africa as early cultivars can provide food and marketable product available from the current growing season, and they can be grown in a diverse array of cropping systems. In addition to escaping drought, early maturing cultivars can escape some insect infestations [38]. Selection for early flowering and maturity and yield testing of breeding lines under water-stressed conditions has been used successfully in developing cowpea cultivars adapted to low rainfall areas [75]. Early maturing cowpea varieties that escape terminal drought have been released and widely accepted by African farmers. But, if exposed to recurrent drought during the vegetative or reproductive stages, these varieties perform very poorly. Efforts are therefore being made to breed cowpea varieties with enhanced drought tolerance for early, mid and terminal season drought stresses.

4.7 Drought Avoidance and Tolerance in Cowpea

In cowpea, two types of drought tolerance have been described at the seedling stage using the wooden box technique [61]. In experiments described by Mai-Kodomi et al. [90], all the seedlings of two susceptible lines TVu 7778 and TVu 8256, were completely dead 15 days after termination of watering. TVu 11979 stopped growth after the onset of drought stress but exhibited a declining turgidity in all tissues of the plants including the unifoliate and the emerging tiny trifoliates for over two weeks. All plant parts such as the growing tip, unifoliates and epicotyls gradually died almost at the same time. Genotypes displaying this type of resistance mechanism were referred to as “Type 1” mode of resistance by Mai-Kodomi et al. [90]. In contrast, the “Type 2” drought tolerant lines like Dan Ila and Kanannado remained green for longer time and continued slow growth of the trifoliates under drought stress with varieties wilting and dying about four weeks after drought stress started. The two types of tolerance responses by cowpea seedlings to drought stress indicate that cowpea genotypes adopted different mechanisms to cope with prolonged drought encountered in the semi-arid regions of Africa where the crop is believed to have originated. Closure of stomata to reduce water loss through transpiration and cessation of growth (for type 1 drought avoidance) and osmotic adjustment and continued slow growth (drought tolerance in type 2) have been recommended as the possible mechanisms for drought tolerance in cowpea [23]. Cowpea is known as dehydration avoider with strong stomata sensitivity and reduced growth rate [23]. This seems to be the mechanism underlying the Type 1 reaction to drought of Tvu 11986 and Tvu 11979.

The type 2 reaction of Dan Illa and Kanannado appears to be a mixture of three mechanisms: stomata regulation (partial opening), osmotic control and selective mobilization with distinct visible differences in the desiccation of lower leaves compared to the upper leaves and growing tips [61]. It seems that the type 2 mechanism of drought tolerance is more effective in keeping the plants alive for a longer time and ensures better chances of recovery than type 1 when the drought spell ends. Both drought tolerant lines Dan Illa and Kanannado are local varieties commonly grown in the Sudano-Sahelian border areas of Nigeria and Niger Republic, indicating that in these areas farmers have selected cowpea varieties with good adaptation to drought. Similarly, Muchero et al. [91] studied 14 genotypes of cowpea at seedling stage and established the presence of significant genetic variation in responses to drought stress. Genotypes, IT93 K-503-1 and IT98 K-499-39 were consistently more tolerant whereas CB46 and Bambey 21 were more susceptible.

Drought-tolerant genotypes, once identified, will open new avenues for indirect selection, either by analysis of their physiological properties [92] and/or by identifying DNA markers for these traits [93]. Several other mechanisms may partially explain the extreme dehydration avoidance of cowpea. The mechanisms through which cowpea is able to resist vegetative-stage drought may be related to the limited decrease of leaf water potential even under extreme drought. The lowest leaf water potential recorded for cowpea is -18 bars (-1.8 Mpa) [94,95], whereas peanut has developed leaf water potentials under drought as low as -82 bars (-8.2 Mpa) [96]. Cowpea also changes the position of leaflets under drought (a drought avoidance mechanism).

They become paraheliotropic and oriented parallel to the sun's rays when subjected to soil drought, causing them to be cooler and thus transpire less [97], which helps to minimize water loss and maintain water potential.

4.8 Transpiration Rate

Transpiration rate per unit of leaf area can be measured with similar equipment as for Net carbon exchange rate (NCER) or can be indirectly assessed with stomatal conductance measurements using a porometer in pea [69]. In field conditions, especially at early stages of the plant life, when plant canopy is not full established, the significance of this measurement for crop water consumption is restricted by the importance of water evaporation from the soil surface receiving solar radiation. Despite this limit, Lacape et al. [98] obtained, in cotton crops, similar relationships of soil drying Fraction of Transpired Soil Water (FTSW)) with stomatal conductance and with daily crop water up take by plants measured with a neutron probe and water balance. Similar results were obtained in pea when comparing stomatal conductance and transpiration measured in pots [99].

4.9 Biomass Yield and Nitrogen Fixation

Among the performance criteria of the crop system, biomass production is undoubtedly the most sensitive to soil water deficit. In a number of experiments in various crop species, even with short and moderate water deficit, a reduction in above-ground vegetative biomass has been observed [70,71,100]. In each of these cases, the major effect of water deficit is probably a sink limitation of biomass production, as expansion of all the phytomers in development in the apical bud is irreversibly reduced, while photosynthesis of mature leaves is maintained, or is less affected during the stress, and restored to the level of the control after the period of water deficit [68,101]. Only when the intensity and/or duration of water deficit are sufficient, does the source limitation become dominant, as photosynthesis and light interception are reduced (by cessation of branching and development of leaves out of the shoot tips; Belaygue et al. [74]. This may explain why current crop models, which are based on source limitation of biomass by water deficit [102], may fail in reproducing the effects of short and moderate soil water deficit on biomass and grain yield. The amount of nitrogen fixed, an important criterion of legume performance in low-input systems, has sensitivity to water deficit that is equal to or even higher than biomass production as it is the result of a reduction in both the biomass and the percentage of nitrogen derived from the atmosphere [103].

4.10 Duration of Flowering

Date of flowering is mainly controlled by temperature and photoperiod and is therefore only affected by water deficit through increased canopy temperature was linked to stomatal closure in cotton [98]. In indeterminate plants the duration of the flowering period is generally reduced by water deficit or moderate heat stress, although a severe but short heat stress inducing flower abortion may increase it, as long as the plant has the ability to recover from the stress [104]. In field conditions, especially in tropical regions, water deficit and heat stress are frequently occurring simultaneously and their effects on the reduction of flowering duration are additive. As shown in cotton and pea, this shortening of the reproductive period by water deficit can be analysed as the result of a higher sensitivity of phytomer appearance compared with flower production, thereby reducing the number of nodes above the last mature leaf and accelerating the cut-out [98].

4.11 Grain Yield and Harvest Index

The importance of maintenance of reproductive development compared with vegetative growth is that harvest index is less affected by water deficit than above-ground biomass, except for severe water deficit occurring after cut out [98]. Similar observations have been made in lupins [105] although attributed to hastening of the reproductive development after a transient water deficit. When soil dehydration occurs after the start of flowering and is sufficient to reduce vegetative sinks (by cessation of branching and reduction of leaf expansion) without reducing light interception (if LAI is already higher than 3) and photosynthesis, grain yield can even be increased by this water deficit, leading to an increase in harvest index [105]. At the same time, the reduction in plant transpiration may be sufficient to induce a significant saving in water and an increase in water-use efficiency for grain production. This suggests that transpiration is reduced in the same proportion as biomass yield, but grain yield can be increased by water stress as long as biomass dry matter is not reduced by 40–50% [106,107].

4.12 Screening Approaches for Drought Tolerance

Two main approaches have been so far used for screening and breeding for drought tolerance in plants. The first is the performance approach that utilizes grain yield and its components as the main criteria, since yield is the integrated expression of the entire array of traits related to productivity under stress [108]. This approach focuses on empirical validation of the yield of varieties over several years and locations in areas with known drought incidence patterns using standard field designs. Significant achievements have been made in developing cowpea varieties with better adaptation to water stress [75,95,108,109,]. Though various cowpea breeding materials such as F_2, F_3 and backcross populations have been used for drought tolerance studies in cowpea, the empirical approach mainly relies on the use of recombinant inbred lines (RIL) to enable the consistent evaluation of performance and understanding of genotype-by-environment interaction, as the intensity and frequency of naturally occurring drought stress are not entirely predictable. The RIL population, developed through single seed descent of several selfed generations consists of individual lines carrying dispersed homozygous segments of a parental chromosome.

The second approach employs analyses of physiological or morphological traits that contribute significantly to growth and yield in the event of drought. These traits include delayed leaf senescence, water-use efficiency, water potential, relative turgidity, leaf gas exchange, relative water content, diffusion pressure deficit, chlorophyll stability index, and carbon isotope discrimination [36,56,110,111,]. For most of these traits, there have been conflicting results on their value in selecting for tolerant varieties in the field [112,113]. Significant contributions of these physiological traits were found typically under extreme water deficit conditions where plant survival rather than yield is the key character of interest [114]. Such extreme conditions are not typically encountered in cowpea production zones of West Africa. Based on the available evidence, it will be sensible to analyse the inherent differences in sensitivity to drought in cowpea by direct assessment of growth and yield components in the field under typical production conditions. Slabbert et al. [115] noted that whenever the physiological approach is used in selecting varieties, their performance should be validated in the field under naturally occurring drought. Agbicodo et al. [85] based on a review of several studies identified the following traits as the more reliable in developing cowpea cultivars with tolerance to drought. These include determination of chlorophyll fluorescence, stomatal conductance measurements, abscisic acid measurements, measuring free proline levels, wooden box screening for drought tolerance at the seedling stage, and delayed leaf senescence.

In the evaluation of several cowpea lines, Muchero et al. [91] identified IT93K503-1 as the most tolerant to drought. Subsequently, highly reproducible quantitative trait locus (QTL) for this trait were mapped in a cowpea recombinant inbred line (RIL) population ‘IT93K503-1 x CB46’ in which 10 QTL regions, *Dro-1* to *Dro-10*, were identified on a genetic linkage map using both screen-house and field-based phenotyping [116].

4.13 Effects of Water Stress on Grain Nutrient Content and Phytochemical Variability in Cowpea Seeds under Contrasting Moisture Conditions

Pulses are a vital source of plant-based proteins and amino acids for people around the globe and may be eaten as part of a healthy diet to address obesity, as well as to prevent and help manage chronic diseases such as diabetes, coronary conditions and cancer; they are also an important source of plant-based protein for animals [6,117]. In a study of the phenolic content and antioxidant properties of selected cowpea varieties tested in bovine peripheral blood. Adjei-Fremah *et.al*. [118] reported that, the potential of cowpea polyphenols to reduce oxidative stress in livestock production is high which is a positive indication for human health improvement. Viets [119] and Alam [120] reported that, drought reduces both nutrient uptake by the roots and transport from the roots to the shoots, because of restricted transpiration rates and impaired active transport and membrane permeability, the decline in soil moisture also results in a decrease in the diffusion rate of nutrients in the soil to the absorbing root surface [121,122]. This will consequently affect the seed yield and the nutritive value of the seed. A study conducted in Pakistan by [6] on the antioxidant activity of the extracts of some cowpea cultivars commonly consumed in Pakistan, revealed that, phenolic constituents contained in cowpea may have a future role as ingredients in the development of functional foods to determine the antioxidant benefits of the cowpea consumed. The assessment of antioxidant potential might be a fruitful approach for advocating them as nutraceuticals, in addition to them being potential protein and carbohydrate sources. The consumption of a processed cowpea would not only improve nutrient utilization, but also provide potential nutraceuticals for human health. It could therefore be concluded that cowpea could contribute significantly in the management and/or prevention of degenerative diseases associated with free radical damage, in addition to their traditional role of preventing protein malnutrition. Therefore, it will be of immense value to determine the antioxidant, phenolic and other nutritional values of cowpea under contrasting moisture regimes for developed cowpea inbred lines in this study.

4.14 Genotype by Environment (G x E) Interaction

Genotype by environment interaction (G x E) can be defined as the differential response of varying genotypes under change(s) in the environment [123]. The ability, or inability, of organisms to adapt to changes in their environment at the speed necessary, determines the continuation, extinction, or evolution of species [124]. Genotype by environmental interaction is an important factor affecting the breeding and stability of improved and elite genotypes developed through plant improvement programmes in both the developed and developing countries [125] including Ghana. A plant cannot migrate when challenged by fluctuations in environmental conditions, which means that it has to cope with environmental heterogeneity by adapting to the new or fluctuating environment [126]. It can do so via changing the phenotypic expression, a phenomenon called ‘phenotypic plasticity’, which is often involves altering gene expression and plant physiology in response to environmental signals [127–129]. Scheiner [130], reported that it is not only phenotypic plasticity trait and developmental stage specific but it also often depends on the genotype. When phenotypic plasticity differs between genotypes, this is described as genotype by environment interaction. Dean [131], reported that environmental factors such as temperature, light intensity, and humidity, are the major cause of genotypic and phenotypic variation. Lande and Shannon [132] reported that genotype by environment interaction has heavy implications on the evolution of species, they further on suggest that in constant or unpredictable environments, genetic variance reduces population mean fitness and increases the risk of extinction. Although the importance of the differential effect of the environment on different plant genotypes has been known for a long time and has been considered in crop-breeding programs, it is generally viewed as a thought-provoking issue. When phenotypic plasticity differs between genotypes, this is described as Genotype by environment interaction. *Gerrano* et al. [133], defined an “ideal” test environment, which is a virtual environment that has the longest vector of all test environments (most discriminating) and is located on the AEC abscissa (most representative). Yan et al. [134] reported that G and GE must be considered simultaneously in mega-environment analysis, genotype evaluation, and test-environment evaluation; separation of G from GE is primarily a mathematical manipulation that is not always supported by biological evidence combining G and GE in GGE biplot analysis is essential for addressing plant breeding and agricultural problems. The performance of a genotype is determined by three factors: genotypic main effect (G), environmental main effect (E) and their interaction [135]. Lin and Binns [136] introduced a new stability concept as yearly variance within test locations (YV) which relates to stability in time (across years). Also, Lin and Binns [137] defined the superiority index (PI) as the genotype general superiority and defined it as the distance mean square between the genotype's response and the maximum response over environments. Multi-locational trials are necessary in order to confirm the distinctiveness, uniformity and stability of newly developed crop varieties in readiness for recommendation to farmers [138]. Understanding of the genetic variability of cowpea is important to design and accelerate conventional breeding programmes [133]. Collection, characterization and evaluation of available cowpea germplasm, quantification of the magnitude of diversity and classification into groups facilitate identification of genetic variability that enables breeders to select traits of interest for an improvement programmme [139, 140]. Therefore, variety trials in a breeding program are usually conducted in several environments, to minimize the risk of discarding genotypes that potentially perform well in some, but not in all, environments; that is, when there is significant G × E and, in particular, when cross-over interaction occurs [141].

4.15 Farmer Preferences, Production Constraints and Perception on Drought in Cowpea

For cowpea varieties with improved tolerance to drought to be accepted by farmers, it is important to solicit their views and get them involved right from the beginning of the research and breeding process to the end to help facilitate their adoption [142]. A major factor that affects production and consumption of cowpea in Ghana is varietal preference [3]. Ghanaians are known to have a high preference for cream seeded cowpea [30].

Production of cowpea with consumer preferred grain type according to Egbadzor et al. [143], can boost cultivation in Ghana. In order to overcome the problem of low productivity, a preamble strategy is to replace the existing low yielding cowpea varieties with newer high yielding varieties, taking into consideration the preference for taste and market requirements.

Farmers' low adoption of technologies developed by research institutions show the need for client-orientation in research and development. The key factors that constrain farmers' adoption of technologies are inappropriateness of the technologies, unavailability of required inputs, and farmers' socio-economic conditions [144]. Therefore, technologies that do not meet farmers' preferences, objectives, and conditions are less likely to be adopted [145]. Farmers are more likely to assess a technology with criteria and objectives that are different from criteria used by scientists. However, farmers' and scientists' criteria for technology assessment must be complementary for effective research and technology development. Farmer evaluations help scientists to design, test, and recommend new technologies to reflect information about farmers' criteria for usefulness of the innovation [146]. In this context, participation is crucial. Participatory research allows incorporation of farmers' indigenous technical knowledge, identification of farmers' criteria and priorities, and definition of research agenda. Participatory Rural Appraisal (PRA) tools were applied to capture farmers' perceptions and fit preferences. De Groote and Bellon [147] and [148], emphasize that participatory approach as Participatory Rural Appraisal (PRA), which involves local people in gathering and analysing information, which allows seeking of insights about local people and their actual conditions, and fosters dialogue between scientists and farmers. By integrating farmers' concerns and conditions into agricultural research, it is hoped that research would develop technologies that become widely adopted, resulting in more productive, stable, equitable, and sustainable agricultural systems.

4.16 Markers in Cowpea Breeding

Modern technologies, such as marker-assisted selection (MAS), in combination with conventional breeding have been successfully used for genetic enhancement of other crop species. The development and use of biochemical-based analytical techniques and molecular marker technologies, such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs), and microsatellites or simple sequence repeats (SSRs), have greatly facilitated the analysis of the structure of plant genomes and their evolution, including relationships among the Legumioseae [1,134, 149]. This in turn has contributed significantly to our current understanding of the cowpea genome organization and evolution. There is a clear need for leveraging modern biotechnological tools to complement conventional breeding in cowpea. Such efforts should focus on the development of molecular markers and protocols for use in marker-assisted selection (MAS) and marker-assisted breeding. [149]. Recently, a Dehydration-Responsive Element-Binding protein2A (DREB2A) ortholog was isolated from cowpea, VuDREB2A (GenBank: JN629045.3) which was highly induced in response to desiccation, heat and salinity, and conferred enhanced drought tolerance by up regulation of several stress-responsive genes in transgenic Arabidopsis [79]. A Ser/Thr-rich region immediately downstream to the DNA binding domain in VuDREB2A appeared to have some role in the stability of the protein, since its removal led to a dwarf phenotype and enhanced expression of some of the downstream genes of VuDREB2A, similar to DREB2A CA [150]. This provides vital clue to the possibilities of existence of similar pathways regulating VuDREB2A in cowpea. A thorough understanding of the molecular mechanisms underlying the stress responses of crop plants, especially tolerant species such as cowpea is necessary for development of enhanced stress-tolerant varieties for sustainable agriculture in the future

5. CONCLUSION

Despite numerous research studies on seedling and reproductive stage drought tolerance in cowpea, the relationship between the two life cycle of cowpea, in relation to the genetic variability for drought, appears to be limited in Ghana, suggesting more research into this area.

COMPETING INTERESTS

Author has declared that no competing interests exist.

REFERENCES

1. Timko MP, Ehlers JD, Roberts PA. Cowpea. In: Kole C, Editor. Pulses, Sugar and Tuber Crops. Springer Berlin Heidelberg. 2007;49–67.
   Available:http://link.springer.com/chapter/10.1007/978-3-540-34516-9_3.
   Accessed 15 Jun 2017.
2. Singh B, Ehlers J, Sharma B, Freire Filho F. Recent progress in cowpea breeding. Fatokun CA, Tarawali SA, Singh BB, Kormawa PM. 2002;22-40.
3. Langyintuo AS, Lowenberg-De Boer J, Faye M, Lambert D, Ibro G, Moussa B, et al. Cowpea supply and demand in West and Central Africa. Field Crops Research. 2003;82:215–231.
4. Quaye W, Adofo K, Madode Y, Abizari A-R. Exploratory and multidisciplinary survey of the cowpea network in the Tolon-Kumbungu district of Ghana: A food sovereignty perspective. African Journal of Agricultural Research. 2009;4:311–320.
5. Khalid II, Elhardallou SB. Factors That Compromise the Nutritional Value of Cowpea Fluor and Its Protein Isolates. Food and Nutrition Sciences. 2016;07: 112–121.
6. Zia-Ul-Haq M, Ahmad S, Amarowicz R, De Feo V. Antioxidant activity of the extracts of some cowpea (*Vigna unguiculata* (L) Walp.) Cultivars Commonly Consumed in Pakistan. Molecules. 2013;18:2005-2017.
7. Patil M, Magan D. Genetic diversity analysis in cowpea (*Vigna unguiculata* (L.) Walp.) by using rapd markers; 2013.
8. Ng N, Marechal R. Cowpea taxonomy, origin and germplasm. Cowpea research, production, and utilization Wiley, Chichester, UK. 1985;11–21.
9. Huynh BL, Close TJ, Roberts PA, Hu Z, Wanamaker S, Lucas MR, et al. Gene pools and the genetic architecture of domesticated cowpea. The Plant Genome. 2013;6.
   DOI: 10.3835/plantgenome2013.03.0005
10. Batieno T. Breeding for drought tolerance in cowpea [*Vigna Unguiculata* (L.) Walp.] Using Marker Assisted Backcrossing; 2014.
11. Flight C. The Kintampo Culture and Its Place in the Economic Prehistory of West Africa. In: Origins of African Plant Domestication. Reprint 2011. Berlin, Boston: De Gruyter Mouton; 1976.
    Available:https://www.degruyter.com/abstract/books/9783110806373/9783110806373.211/9783110806373.211.xml.
    Accessed 28 Sep 2017
12. Padulosi S, Ng N. Origin, taxonomy, and morphology of *Vigna unguiculata* (L.)

Walp. Advances in Cowpea Research. 1997;1–12.
13. Verdcourt B. Studies in the Leguminosae-papilionoideae for the'Flora of Tropical East Africa': II. Kew Bulletin. 1970;235–307.
14. Fang J, Chao C-CT, Roberts PA, Ehlers JD. Genetic diversity of cowpea [<Emphasis Type="Italic">Vigna unguiculata</Emphasis> (L.) Walp.] in four West African and USA breeding programs as determined by AFLP analysis. Genet Resour Crop Evol. 2007;54:1197–209.
15. Faris DG. The origin and evolution of the cultivated forms of *Vigna Sinensis*. Can J Genet Cytol. 1965;7:433–52.
16. Steele W. Cowpeas. Evolution of Crop Plants. 1976;183–5.
17. Coulibaly O, Lowenberg-Deboer J. The economics of cowpea in West Africa. 2002; 351–66.
18. Verdcourt B. Studies in the Leguminosae-papilionoideae for the'Flora of Tropical East Africa': II. Kew Bulletin. 1970;235–307.
19. Jindla LN, Singh KB. Inheritance of flower colour, leaf shape and pod length in cowpea (*Vigna sinensis* L.). Indian Journal of Heredity. 1970;2:45–49.
20. Agbicodo EM, Fatokun CA, Muranaka S, Visser RGF, Der CGL van. Breeding drought tolerant cowpea: Constraints, accomplishments, and future prospects. Euphytica. 2009;167:353–370.
21. Obiegbuna JE, Ameh A, Morah GN. A comparative study of the effects of steaming and rehydration on the acceptability of akara from cowpea and African yambean meals. Journal of Sustainable Agriculture and the Environment. 2006;8:65–72.
22. Singh BB, Ishiyaku MF. Brief communication. Genetics of rough seed coat texture in cowpea. Journal of Heredity. 2000;91:170–174.
23. Umar L. Breeding for grain quality traits in cowpea [*Vigna Unguiculata* (L) Walp]; 2014.
24. Xu P, Hu T, Yang Y, Wu X, Wang B, Liu Y, et al. Mapping genes governing flower and seedcoat color in Asparagus bean (Vigna unguiculata ssp. sesquipedalis) based on single nucleotide polymorphism and simple sequence repeat markers. Hort Science. 2011;46:1102–4.
25. Ogbuinya PO. Advances in Cowpea Research. Biotech Develop Monitor. 1997; 33:1012.
26. Tan H, Tie M, Luo Q, Zhu Y, Lai J, Li H. A review of molecular makers applied in Cowpea (*Vigna unguiculata* L. Walp.) Breeding. Journal of Life Sciences. 2012; 6:1190.
27. Fatokun CA, Boukar O, Muranaka S. Evaluation of cowpea (Vigna unguiculata (L.) Walp.) germplasm lines for tolerance to drought. Plant Genetic Resources. 2012;10:171–6.
28. Awunyo-Vitor D, Bakang J, Cofie S. Estimation of farm level technical efficiency of small-scale cowpea production in Ghana. 2013.
Available:http://ir.knust.edu.gh:8080/handle/123456789/6140.
Accessed 10 Dec 2017
29. Awunyo-Vitor D, Bakang J, Cofie S. estimation of farm level technical efficiency of small-scale cowpea production in Ghana. 2013.
Available:http://ir.knust.edu.gh:8080/handle/123456789/6140
Accessed 10 Dec 2017
30. Quaye W, Adofo K, Madode Y, Abizari AR. Exploratory and multidisciplinary survey of the cowpea network in the Tolon-Kumbungu district of Ghana: A food sovereignty perspective. African Journal of Agricultural Research. 2009;4:311–320.
31. Adu-Dapaah H, Afum J, Asumadu H, Gyasi-Boakye S, Oti-Boateng C, Padi H. Cowpea Production Guide. Kumasi: Ministry of Food and Agriculture (MOFA) Food crops Development Project (FCDP) Accra, Ghana; 2005.
32. SARI. Annual Report 2002. 2002. Available:http://www.csir.org.gh/images/CSIR-SARI_Reports/NEW%20CSIR-SARI%20Annual%20Report%202014%20Final.pdf.
Accessed 5 Dec 2017
33. Singh BB. Advances in Cowpea Research. IITA; 1997.
34. Padi FK. Genotype × environment interaction and yield stability in a cowpea-based cropping system. Euphytica. 2007; 158:11–25.
35. Bates LM, Hall AE. Stomatal closure with soil water depletion not associated with changes in Bulk leaf water status. Oecologia. 1981;50:62–65.

36. Gwathmey CO, Hall AE. Adaptation to midseason drought of cowpea genotypes with contrasting senescene traits. Crop Science. 1992;32:773.
37. Padi FK. Response to selection for grain yield and correlated response for grain size and earliness in cowpea based on early generation testing. Annals of Applied Biology. 2008;152:361–368.
38. Ehlers JD, Hall AE. Cowpea (*Vigna unguiculata* L. Walp.). Field Crops Research. 1997;53:187–204.
39. Ahmed FE, Suliman ASH. Effect of water stress applied at different stages of growth on seed yield and water-use efficiency of cowpea. Agriculture and Biology Journal of North America. 2010; 1:534–540.
40. Padi F. Relationship between stress tolerance and grain yield stability in cowpea. The Journal of Agricultural Science. 2004;142:431–443.
41. Singh BB. Advances in Cowpea Research. IITA; 1997.
42. Rachie K, Silvestre P. Grain legumes. Food crops of the lowland tropics. 1977; 41–74.
43. Emechebe A, Florini D. Shoot and pod diseases of cowpea induced by fungi and bacteria. Advances in cowpea research International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. 1997; 176–192.
44. Ahmed FE, Hall AE, Madore MA. Interactive effects of high temperature and elevated carbon dioxide concentration on cowpea [*Vigna unguiculata* (L.) Walp.]. Plant, Cell & Environment. 1993;16:835–842.
45. Warrag MOA, Hall AE. Reproductive responses of cowpea (*Vigna unguiculata* (L.) Walp.) to heat stress. II. Responses to night air temperature. Field Crops Research. 1984;8:Supplement C:17–33.
46. Ahmed FE, Hall AE, DeMason DA. Heat injury during floral development in cowpea (*Vigna unguiculata*, Fabaceae). American Journal of Botany. 1992;784–791.
47. Mutters R, Mannheim W, Bisgaard M. Taxonomy of the group. Pasturella and pasteurellosis/Edited by Adlam C, Rutter JM; 1989.
48. Kay DE. Food legumes. Food legumes; 1979.
49. Summerfield R, Roberts E. *Vigna unguiculata*. A Handbook of Flowering, CRC Press, Boca Raton, FL, USA. 1985; 171–184.
50. Singh B, Mai-Kodomi Y, Terao T. A simple screening method for drought tolerance in cowpea. The Indian Journal of Genetics and Plant Breeding. 1999;59:211–220.
51. Singh S, Jackai L. Insect pests of cowpeas in Africa: Their life cycle, economic importance and potential for control. Cowpea research, production and utilization. 1985;217–231.
52. Stanton BJ, Villar M. Controlled reproduction of Populus. Biology of Populus and its implications for management and conservation, part I NCR Research Press, National Research Council of Canada, Ottawa. 1996;113–138.
53. Ismail A, Hall A, Bray E. Drought and pot size effects on transpiration efficiency and carbon isotope discrimination of cowpea accessions and hybrids. Functional Plant Biology. 1994;21:23–35.
54. Shackel KA, Hall AE. Comparison of water relations and osmotic adjustment in sorghum and cowpea under field conditions. Functional Plant Biology. 1983; 10:423–435.
55. Watanabe I, Hakoyama S, Terao T, Singh B. Evaluation methods for drought tolerance of cowpea. Advances in cowpea research. 1997;141–146.
56. Bates LM, Hall AE. Stomatal closure with soil water depletion not associated with changes in Bulk leaf water status. Oecologia. 1981;50:62–65.
57. Turk KJ, Hall AE. Drought adaptation of cowpea. II. Influence of drought on plant water status and relations with seed yield. Agronomy Journal. 1980;72:421–427.
58. Ziska L, Hall A, Hoover R. Irrigation management methods for reducing water use of cowpea (*Vigna unguiculata* [L.] Walp.) and lima bean (*Phaseolus lunatus* L.) while maintaining seed yield at maximum levels. Irrigation Science. 1985; 6:223–239.
59. Akyeampong E. Some responses of cowpea to drought stress - Google Scholar; 1989
Available:https://scholar.google.com/scholar?q=Akyeampong,+E.+(1989).+Some+responses+of+cowpea+to+drought+stress&hl=en&as_sdt=0&as_vis=1&oi=scholart&sa=X&ved=0ahUKEwiZ2fn93_PUAhVmD8AKHXiNC7oQgQMIHjAA
Accessed 6 Jul 2017.
60. Gwathmey CO, Hall AE. Adaptation to Midseason drought of cowpea genotypes

with contrasting senescene traits. Crop Science. 1992;32:773.
61. Mai-Kodomi Y, Singh B, Terao T, Myers Jr O, Yopp J, Gibson P. Inheritance of drought in cowpea. Indian Journal of Genetics. 1999;59:317–323.
62. Hall A, Singh B, Ehlers J. Cowpea breeding. Plant Breeding Reviews. 1997; 15:215–274.
63. Summerfield R, Roberts E. Vigna unguiculata. A Handbook of Flowering, CRC Press, Boca Raton, FL, USA. 1985; 171–84.
64. Minchin F, Summerfield R. Symbiotic nitrogen fixation and vegetative growth of cowpea (*Vigna unguiculata* (L.) Walp.) in waterlogged conditions. Plant and Soil. 1976;45:113–27.
65. Hsiao TC. Plant responses to water stress. Annual review of plant physiology. 1973; 24:519–70.
66. Karamanos A. Water stress and leaf growth of field beans (*Vicia faba* L.) in the field: leaf number and total leaf area. Annals of Botany. 1978;42:1393–402.
67. Ney B, Wery J. How does a grain legume crop work? A simulation model to integrate our knowledge and to solve agronomic problems. 1998;19.
68. Guilioni L, Wéry J, Lecoeur J. High temperature and water deficit may reduce seed number in field pea purely by decreasing plant growth rate. Functional Plant Biology. 2003;30:1151–1164.
69. Lecoeur J, Wery J, Turc O, Tardieu F. Expansion of pea leaves subjected to short water deficit: Cell number and cell size are sensitive to stress at different periods of leaf development. Journal of Experimental Botany. 1995;46:1093–1101.
70. Lacape M, Wery J, Annerose D. Relationships between plant and soil water status in five field-grown cotton (*Gossypium hirsutum* L.) cultivars. Field Crops Research. 1998;57:29–43.
71. Belaygue C, Wery J, Cowan A, Tardieu F. Contribution of leaf expansion, rate of leaf appearance, and stolon branching to growth of plant leaf area under water deficit in white clover. Crop Science. 1996; 36:1240–1246.
72. Pellegrino A, Lebon E, Voltz M, Wery J. Relationships between plant and soil water status in vine (*Vitis vinifera* L.). Plant and Soil. 2004;266(1/2):129–142.
73. Pellegrino A, Lebon E, Simonneau T, Wery J. Towards a simple indicator of water stress in grapevine (*Vitis vinifera* L.) based on the differential sensitivities of vegetative growth components. Australian Journal of Grape and Wine Research. 2005;1:306-315.
74. Belaygue C, Wery J, Cowan A, Tardieu F. Contribution of leaf expansion, rate of leaf appearance, and stolon branching to growth of plant leaf area under water deficit in white clover. Crop Science. 1996; 36:1240–6.
75. Hall AE, Patel P. Breeding for resistance to drought and heat. Cowpea research, production and utilization Wiley, New York. 1985;137–151.
76. Hall AE, Patel P. Breeding for resistance to drought and heat. Cowpea research, production and utilization Wiley, New York. 1985;137–151.
77. Wien H. The cowpea (*Vigna Unguiculata* (L.) Walp.); 1984.
78. Ashley GM, Hamilton TD. Fluvial response to late Quaternary climatic fluctuations, central Kobuk Valley, northwestern Alaska. Journal of Sedimentary Research. 1993; 63.
79. Sadhukhan A, Panda SK, Sahoo L. The cowpea RING ubiquitin ligase VuDRIP interacts with transcription factor VuDREB2A for regulating abiotic stress responses. Plant Physiology and Biochemistry. 2014;83:51–56.
80. Batieno T. Breeding for Drought Tolerance in Cowpea [*Vigna Unguiculata* (L.) Walp.] Using Marker Assisted Backcrossing; 2014.
81. Bahar MB, Yildirim M. Heat and drought resistances criteria in spring bread wheat: Drought resistance parameters. Scientific Research and Essays. 2010;5:1742–5.
82. Batieno BJ, Danquah E, Tignegre J-B, Huynh BL, Drabo I, Close TJ, et al. Application of marker-assisted backcrossing to improve cowpea (*Vigna unguiculata* L. Walp) for drought tolerance. Journal of Plant Breeding and Crop Science. 2016;8:273–286.
83. Gaur PM, Krishnamurthy L, Kashiwagi J. Improving drought-avoidance root traits in chickpea (*Cicer arietinum* L.) -Current Status of Research at ICRISAT. Plant Production Science. 2008;11:3–11.
84. Mitra J. Genetics and genetic improvement of drought resistance in crop plants. Current Science. 2001;80:758–63.
85. Agbicodo EM, Fatokun CA, Muranaka S, Visser RGF, Der CGL van. Breeding

drought tolerant cowpea: Constraints, accomplishments, and future prospects. Euphytica. 2009;167:353–70.
86. Yancey PH, Clark ME, Hand SC, Bowlus RD, Somero GN. Living with water stress: evolution of osmolyte systems. Science. 1982;217:1214–1222.
87. Hartung W, Schiller P, Dietz K-J. Physiology of poikilohydric plants. In: Progress in botany. Springer. 1998;299–327.
88. Mortimore M, Singh B, Harris F, Blade S. Cowpea in traditional cropping systems. Advances in Cowpea Research. 1997;99.
89. Singh B. Recent genetic studies in cowpea. Challenges and opportunities for enhancing sustainable cowpea production International Institute of Tropical Agriculture, Ibadan, Nigeria. 2002;3–13.
90. Mai-Kodomi Y, Singh BB, Myers O, et al. Two mechanisms of drought tolerance in cowpea. Indian Journal of Genetics & Plant Breeding. 1999;59:309–16.
91. Muchero W, Ehlers JD, Roberts PA. Seedling stage drought-induced phenol-types and drought-responsive genes in diverse cowpea genotypes. Crop Science. 2008;48:541.
92. Schneider KA, Brothers ME, Kelly JD. Marker-assisted selection to improve drought resistance in common bean. Crop Science. 1997;37:51–60.
93. Schneider KA, Brothers ME, Kelly JD. Marker-assisted selection to improve drought resistance in common bean. Crop Science. 1997;37:51–60.
94. Hall A, Schulze ED. Stomatal response to environment and a possible interrelation between stomatal effects on transpiration and CO2 assimilation. Plant, Cell & Environment. 1980;3:467–474.
95. Turk KJ, Hall AE, Asbell C. Drought adaptation of cowpea. I. Influence of drought on seed yield. Agronomy Journal. 1980;72:413–420.
96. Turner NC, Wright GC, Siddique K. Adaptation of grain legumes (pulses) to water-limited environments. Advances in Agronomy. 2001;71:193–231.
97. Schakel K, Hall AE. Reversible leaflet movements in relation to drought adaptation of cowpeas, *Vigna unguiculata* (L.) Walp. Functional Plant Biology. 1979; 6:265–276.
98. Lacape M, Wery J, Annerose D. Relationships between plant and soil water status in five field-grown cotton (*Gossypium hirsutum* L.) cultivars. Field Crops Research. 1998;57:29–43.
99. Lecoeur J, Sinclair T. Field pea transpiration and leaf growth in response to soil water deficits. Crop Science. 1996; 36:331–335.
100. Wakrim Mezrioui R, Wery J. Interrelationship between soil water, grain yield and nitrogen fixation in chickpeas (*Cicer arietinum* L.). Colloques de l'INRA (France); 1995.
101. Lecoeur J, Guilioni L. Rate of leaf production in response to soil water deficits in field pea. Field Crops Research. 1998; 57:319–328.
102. Brisson N, Wery J, Boote K. Fundamental concepts of crop models illustrated by a comparative approach. Working with Dynamic Crop Models, Elsevier, Amsterdam. 2006;257–279.
103. Gregory PJ, Wery J, Herridge DF, Bowden W, Fettell N. Nitrogen Nutrition of Legume Crops and Interactions with Water. In: Linking Research and Marketing Opportunities for Pulses in the 21st Century. Springer, Dordrecht; 2000;335–346.
Available:https://link.springer.com/chapter/10.1007/978-94-011-4385-1_30.
Accessed 10 Dec 2017
104. Guilioni L, Wery J, Tardieu F. Heat stress-induced abortion of buds and flowers in pea: is sensitivity linked to organ age or to relations between reproductive organs? Annals of Botany. 1997;80:159–68.
105. French R, Turner N. Water deficits change dry matter partitioning and seed yield in narrow-leafed lupins (*Lupinus angustifolius* L.). Australian Journal of Agricultural Research. 1991;42:471–484.
106. Blum A. Genetic and physiological relationships in plant breeding for drought resistance. Agricultural water management. 1983;7:195–205.
107. Blum A. Plant Breeding for Water-Limited Environments. Springer Science & Business Media; 2010.
108. Hall A, Singh B, Ehlers J. Cowpea breeding. Plant Breeding Reviews. 1997; 15:215–274.
109. Selvaraj U, Annappan R, Giridharan S. A new high yielding drought tolerant cowpea variety. Madras Agric J. 1986;73:125–128.
110. Hall AE. Phenotyping cowpeas for adaptation to drought. Frontiers in physiology. 2012;3.

111. Anyia AO, Herzog H. Water-use efficiency, leaf area and leaf gas exchange of cowpeas under mid-season drought. European Journal of Agronomy. 2004;20: 327–339.
112. Slabbert R, Spreeth M, Krüger GHJ, Bornman CH. Drought tolerance, traditional crops and biotechnology: breeding towards sustainable development. South African Journal of Botany. 2004;70:116–123.
113. Cruz de Carvalho MH, Laffray D, Louguet P. Comparison of the physiological responses of *Phaseolus vulgaris* and *Vigna unguiculata* cultivars when submitted to drought conditions. Environmental and Experimental Botany. 1998;40:197–207.
114. Serraj R, Sinclair TR. Osmolyte accumulation: Can it really help increase crop yield under drought conditions? Plant, Cell & Environment. 2002;25:333–341.
115. Slabbert R, Spreeth M, Krüger GHJ, Bornman CH. Drought tolerance, traditional crops and biotechnology: breeding towards sustainable development. South African Journal of Botany. 2004;70:116–23.
116. Muchero W, Roberts PA, Diop NN, Drabo I, Cisse N, Close TJ, et al. Genetic architecture of delayed senescence, biomass, and grain yield under drought stress in cowpea. PLoS ONE. 2013;8: e70041.
117. Adjei-Fremah S, Jackai LEN, Schimmel K, Worku M. Microarray analysis of the effect of cowpea (*Vigna unguiculata*) phenolic extract in bovine peripheral blood. Journal of Applied Animal Research. 2015;46: 100–106.
118. Adjei-Fremah S, Jackai LEN, Schimmel K, Worku M. Microarray analysis of the effect of Cowpea (*Vigna unguiculata*) phenolic extract in bovine peripheral blood. Journal of Applied Animal Research. 2015;46: 100–6.
119. Viets IU. FG Water deficits and nutrient availability. Water deficits and plant growth New York, Academic Press. 1972;197: 217–39.
120. Alam SM. Nutrient uptake by plants under stress conditions. Handbook of plant and crop stress. 1999;2:285–313.
121. Alam SM. Nutrient uptake by plants under stress conditions. Handbook of plant and crop stress. 1999;2:285–313.
122. Pinkerton A, Simpson J. Interactions of surface drying and subsurface nutrients affecting plant growth on acidic soil profiles from an old pasture. Australian Journal of Experimental Agriculture. 1986;26:681–689.
123. Mather K, Caligari PS. Genotype and environment interactions. I. Regression of interaction on overall effect of the environment. Heredity. 1974;33:43–59.
124. Barrett RD, Rogers SM, Schluter D. Environment specific pleiotropy facilitates divergence at the Ectodysplasin locus in threespine stickleback. Evolution. 2009; 63:2831–2837.
125. Sabaghnia N, Karimizadeh R, Mohammadi M. Genotype by environment interaction and stability analysis for grain yield of lentil genotypes. Žemdirbyst. 2012;99:305–312.
126. El-Soda M, Malosetti M, Zwaan BJ, Koornneef M, Aarts MG. Genotype× environment interaction QTL mapping in plants: lessons from Arabidopsis. Trends in Plant Science. 2014;19:390–398.
127. Juenger TE. Natural variation and genetic constraints on drought tolerance. Current Opinion in Plant Biology. 2013;16:274–281.
128. Nicotra AB, Segal DL, Hoyle GL, Schrey AW, Verhoeven KJ, Richards CL. Adaptive plasticity and epigenetic variation in response to warming in an Alpine plant. Ecology and evolution. 2015;5:634–647.
129. Van Kleunen M, Fischer M. Constraints on the evolution of adaptive phenotypic plasticity in plants. New Phytologist. 2005; 166:49–60.
130. Scheiner SM, Holt RD. The genetics of phenotypic plasticity. X. Variation versus uncertainty. Ecol Evol. 2012; 2:751–67.
131. Dean AM. A molecular investigation of genotype by environment interactions. Genetics. 1995;139:19–33.
132. Lande R, Shannon S. The role of genetic variation in adaptation and population persistence in a changing environment. Evolution. 1996;50:434–7.
133. Gerrano AS, Adebola PO, van Rensburg WSJ, Laurie SM. Genetic variability in cowpea (*Vigna unguiculata* (L.) Walp.) genotypes. South African Journal of Plant and Soil. 2015;32:165–74.
134. Yang R-C, Crossa J, Cornelius PL, Burgueño J. Biplot analysis of genotype× environment interaction: Proceed with caution. Crop Science. 2009;49:1564–1576.

135. Yang J, Zhu J, Williams RW. Mapping the genetic architecture of complex traits in experimental populations. Bioinformatics. 2007;23:1527–1536.
136. Lin C, Binns M. A method of analyzing cultivar x location x year experiments: A new stability parameter. TAG Theoretical and Applied Genetics. 1988;76:425–30.
137. Lin C, Binns M. Genetic properties of four types of stability parameter. TAG Theoretical and Applied Genetics. 1991; 82:505–9.
138. Nwangburuka C, Denton O. Genotype x Environment Interaction and seed yield stability in cultivated okra using Additive Main Effect and Multiplicative Interaction (AMMI) and Genotype and Genotype × Environment Interaction (GGE). Archives of Applied Science Research. 2011;3: 193–205.
139. Mohammadi S, Prasanna B. Analysis of genetic diversity in crop plants—salient statistical tools and considerations. Crop science. 2003;43:1235–1248.
140. Vanderborght T. A centralized database for the common bean and its use in diversity analysis. In: Genetic Resources of Phaseolus Beans. Springer; 1988;51–65.
141. Kang MS. Using genotype-by-environment interaction for crop cultivar development. Advances in agronomy. 1997;62:199–252.
142. Thagana WM, Gethi M, Mursoy R, Rao G, Silim S. Chickpea: A promising new food legume crop for drought prone cool areas of Kenya. 9th African Crop Science, Conference Proceedings, Cape Town, South Africa. 2009;2009:777–780.
143. Egbadzor K, Yeboah M, Offei S, Ofori K, Danquah E. Farmers key production constraints and traits desired in cowpea in Ghana. Journal of Agricultural Extension and Rural Development. 2013;5:14–20.
144. Singhal A, Dearing JW. Communication of innovations: A journey with Ev Rogers. Sage; 2006.
145. Upton M. African farm management. CUP Archive; 1987.
146. Ashby JA. The effects of different types of farmer participation on the management of on-farm trials. Agricultural administration and extension. 1987;25:235–252.
147. De Groote H, Bellon M. Farmers' participatory research: Application for breeders. 2000;9–11.
148. Bunyatta D, Nyambati E. Participatory evaluation of the production and utilisation of improved forages under different fertiliser regimes, Keiyo District; 1996.
149. Huynh BL, Matthews WC, Ehlers JD, Lucas MR, Santos JRP, Ndeve A, et al. A major QTL corresponding to the Rk locus for resistance to root-knot nematodes in cowpea (*Vigna unguiculata* L. Walp.). TAG Theoretical and Applied Genetics Theoretische Und Angewandte Genetik. 2016;129:87–95.
150. Kongjaimun A, Kaga A, Tomooka N, Somta P, Vaughan DA, Srinives P. The genetics of domestication of yardlong bean, *Vigna unguiculata* (L.) Walp. ssp. unguiculata cv.-gr. sesquipedalis. Annals of Botany. 2012; 109:1185–1200.

Peer-review history:
The peer review history for this paper can be accessed here:
http://www.sdiarticle3.com/review-history/47706