

**Genetic variability for flowering time, maturity and drought tolerance in cowpea [*Vigna unguiculata* (L.) Walp.]: a review paper.**

**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, EUPHETICA 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.

**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.

31 **Keywords:** [*Vigna unguiculata* (L.) Walp.], drought, phenology, markers and participatory  
32 rural appraisal

33

### 34 **Introduction**

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

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

49 In many parts of West Africa, cowpea hay is also critical in the feeding of animals during the dry  
50 season, in addition, cowpea is a nitrogen-fixing plant, when used in rotation with cereal crops it  
51 can help restore soil fertility. Therefore, cowpea can play an important role in the development  
52 of agriculture [6].

53

54 **Origin, domestication and taxonomy of cowpea**

55 The name cowpea probably originated from the fact that the plant was an important source of  
56 hay for cows in the south-eastern United States and in other parts of the world [1]. Speculations  
57 on the origin and domestication of cowpea [*Vigna unguiculata* (L.) Walp.] have been based on  
58 botanical and cytological evidence, information on its geographical distribution as well as  
59 cultural practices and historical records [7].

60 Huynh *et al.* [8] reported that cowpea first moved from West Africa to the World with African  
61 people during the slave-trading period. However, no documentation occurred to support the  
62 extent of the movement. Other researchers also believe that cowpea originated from West Africa,  
63 although the exact location of the centre of origin of the species is not known. Huynh *et al.* [8]  
64 used SNP markers to study the gene pool structure of African wild annual cowpea *V. unguiculata*  
65 subsp. *dekindtiana* from both East and West Africa and to determine their kinship or how they  
66 are related to African wild cowpeas and non-African domesticated cowpeas. These authors found  
67 that out the genetic materials diverged into two gene pools. In a related study, Batiemo [9]  
68 reported that, the two gene pools were distributed in two distinct geographical zones separated  
69 by the dense and vast rainforests of the Congo River basin. In a related study, cowpea remains  
70 were discovered from Kintampo in Ghana and carbon dated to about 1400 - 1480 BC making it  
71 the oldest archaeological evidence of the crop [10].

72 A study which also utilized over 10,000 accessions of world collection at the International  
73 Institute of Tropical Agriculture (IITA) discovered that the collection from West Africa spread to  
74 India by 2000 BC [11]. It was introduced into Europe by the Greeks and Romans who grew it  
75 under the name *Phaseolus*. It was introduced into the Americas relatively more recently. The  
76 research work carried out by IITA showed that germplasm accessions from West Africa showed

77 greater diversity than those from East Africa [11]. These studies provided further evidence that  
78 West Africa was the primary centre of domestication. The centre of maximum diversity of  
79 cultivated cowpea is found in West Africa, encompassing the Savanna regions of Nigeria,  
80 southern Benin, Togo, and north-west part of Cameroon [7]. Verdcourt [12] reported that *Vigna*  
81 has several species, but the exact number varies according to different authors.

82 The cultivated cowpea is grouped under subspecies *unguiculata*, which is further subdivided into  
83 four cultivar groups namely; *unguiculate* which is the common form; biflora or *catjang* which is  
84 characterised by small erect pods and found mostly in Asia, and *sesquipedalis*, or yard-long  
85 bean, also found in Asia and characterised by its very long pods which are consumed as green  
86 'bean'; and *textilis*, found in West Africa and which was used for fibre obtained from its long  
87 peduncles [7].

88 The cultivar group *unguiculata* is the most diverse of the four and is widely grown in Africa,  
89 Asia and Latin America (Fang *et al.*, 2007). Subspecies *unguiculata* is the only cultivated  
90 cowpea, while the other three are wild relatives. Several studies have shown that cowpea was  
91 probably domesticated by African farmers [14] and assumed to have evolved in Africa, because  
92 wild cowpeas only exist in Africa and Madagascar [15]. Although the centre of diversity of wild  
93 *Vigna* species is in south-eastern Africa, West Africa is a major centre of diversity of cultivated  
94 cowpea [11]. Coulibaly and Lowenberg-De Boer [16] used data from amplified fragment length  
95 polymorphism (AFLP) marker analyses of cowpea accessions to hypothesize that cowpea  
96 domestication occurred in north-eastern Africa and could have occurred at the same time with  
97 the domestication of sorghum and pearl millet in the third millennium B.C. [15].

98 | Evolution processes of *V. unguiculata*— resulted in a change in growth habit, that is, from  
99 perennial to an annual breeding crop and from predominantly out-breeding to inbreeding. The  
100 cultivated cowpea evolved through domestication and selection [11].

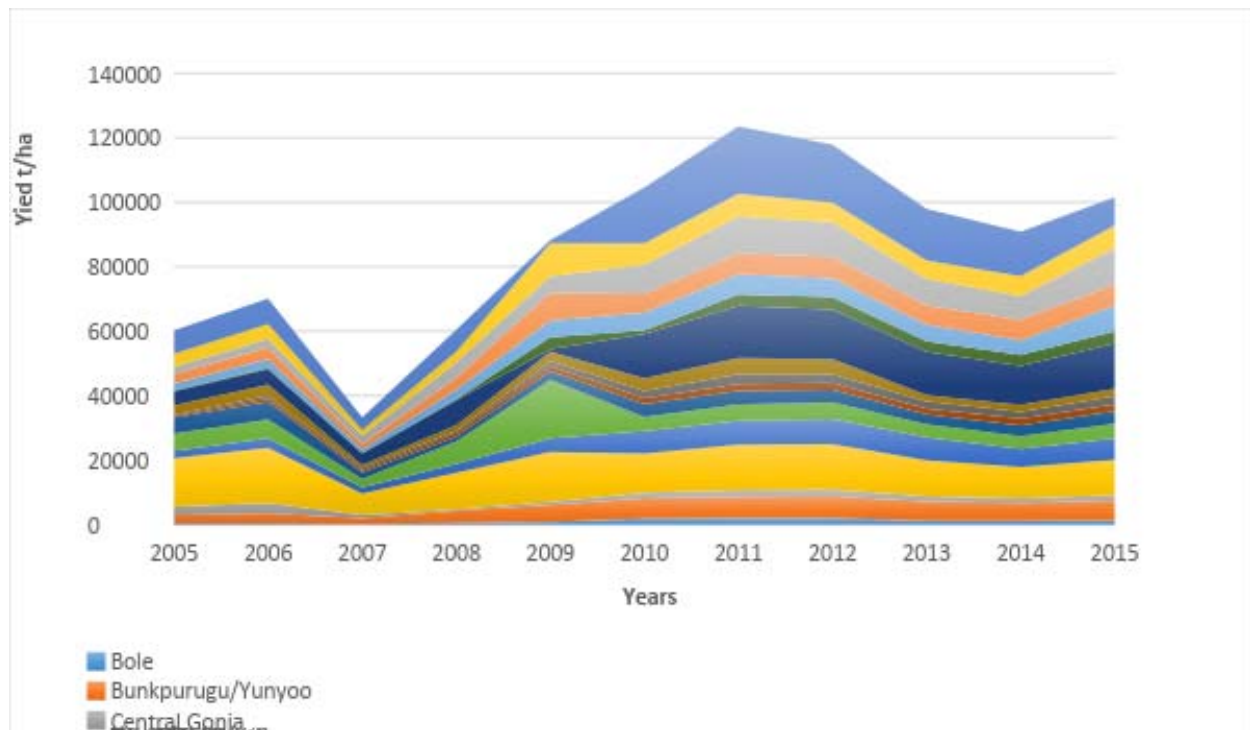
101 Huynh *et al.* [8] reported that cowpea is a diploid crop with 11 pairs of chromosomes ( $2n = 2x =$   
102  $22$ ) and 630 Mb genome size. Cowpea is a *Dicotyledonea* belonging to order *Fabales*, family  
103 *Fabaceae*, subtribe *Phaseolinae*, genus *Vigna*, and section *catiang* [17, 7]. The subspecies  
104 include: *unguiculata*, *stenophylla*, *dekindtiana* and *tenuis* [7].

### 105 **Plant characteristics**

106 The plant is herbaceous and may be erect, prostrate or twinning. The flowers may be purple,  
107 yellow, pink or blue. The pods may be black, purple or cream when dry and hang downwards,  
108 pointing upwards or sideways. Pod length of up to 60 cm has been recorded [18]. Seeds may be  
109 white, cream, purple, red, and brown, mottle brown or black in colour. Four types of grain coat  
110 texture have been identified in cowpea: smooth, rough, wrinkled and loose [19]. Preference for  
111 grain coat texture differs across various parts of the world. For instance, cowpeas with large  
112 white or brown grains with rough grain coat are preferred throughout West Africa, whereas in  
113 East Africa they prefer medium size, brown or red grains with smooth grain coat. In some Latin  
114 American countries, principally Cuba and part of Caribbean, black colour with various categories  
115 of grain coat texture are preferred [20]. In West and Central Africa, rough grain coat is preferred  
116 since it permits easy removal of the grain coat which is essential for indigenous food  
117 preparations [21]. Umar [22] reported that the preference for cowpea grain with rough grain coat  
118 in Nigeria is due to their ease of dehulling and greater expansion capacity. Grain coat colour is  
119 also considered as one of the useful phenotypic markers in cowpea breeding due to its stable  
120 expression and suitability for observation [23].

## 121 **Cowpea production and distribution**

122 Cowpea is cultivated throughout the African continent as well as in some parts of South East  
123 Asia and Latin America. Though native to West Africa, this legume has become a part of the diet  
124 of about 110 million people [24]. In West Africa, cowpea has become an integral part of the  
125 farming systems [24]. Cowpea production in the world was estimated at 12.5 million hectares,  
126 with an annual output of more than 3 million tons [25]. Africa alone produces about 83% of the  
127 world output. Nigeria is the largest world's producer (45.76%), followed by Niger (15%), Brazil  
128 (12%), and 5 % for Burkina Faso [26], with Africa's arid Sahel region accounting for 64%. In  
129 Ghana, cowpea cultivation is primarily done in the northern and upper West regions. Cowpea  
130 commercial regions include the Upper East, Brong Ahafo, Eastern, Volta and Ashanti. The  
131 Ghana government policy objective for the cowpea subsector is to encourage increased  
132 production so that self-reliance and food security can be achieved. Yet, the production of the  
133 crop has fluctuated over the years partly due to climatic conditions and policy issues [27].  
134 Average yield of cowpea in Ghana is 1,3 t/ha with a potential estimated at 1.96 t/ha [28].  
135 Cowpea farming serves as a vital component of sustainable cropping system in Ghana because of  
136 its nitrogen fixing ability and socio-cultural values [29]. The crop is considered drought and heat  
137 tolerant, and is able to fix nitrogen up to 240 t/ha and leaving about 60–70 kg nitrogen for the  
138 following crops [30]. Production is mainly done by small-scale resource-poor farmers practicing  
139 mostly peasant agriculture and growing largely unimproved varieties resulting in low output.  
140 SARI [31] carried out studies, which showed an adoption rate per annum of 3.9 % for improved  
141 varieties in northern Ghana, confirming that majority of farmers still grow landraces or  
142 unimproved varieties of the crop.



143

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

145

### 146 **Climate and soil requirements for cowpea production**

147 Cowpea is predominantly a hot weather crop grown in many parts of the tropical world (Singh,  
 148 1997). It thrives well between the temperature ranges of 20-35 °C, since temperature above 35°C,  
 149 is known to reduce yield. Heat stress is often defined as a situation where temperatures are high  
 150 enough for sufficient period that can cause irreparable dam [33, 34] age to the plant function or  
 151 development which shortens the time for photosynthesis to contribute to seed production [35].  
 152 Comparison of cowpea growth and grain yield under tropical and subtropical conditions have  
 153 shown that high temperature is an important stress factor for cowpea [36, 35]. Many stages of the  
 154 crop are sensitive to high temperature [37, 38]. In general, higher temperatures shorten the period  
 155 of reproductive growth, and grain yield is consequently reduced. In addition to warmer  
 156 temperatures accelerating crop development, high temperatures also allow little time for carbon  
 157 assimilation that could be partitioned to the grain and substantially reduces yield [39]. Singh [40]

158 reported that flower and pod shedding also increase at temperatures above 35°C leading to a  
159 marked reduction in yield. Cowpea requires a rainfall of 600 to 800 mm per annum for optimum  
160 growth and development. Medium and long duration types require a rainfall between 600 and  
161 1500 mm per annum [41]. Excessive rain or atmospheric humidity results in reduction in yield  
162 due to a high incidence of fungal diseases [42].

163 High night temperatures appear to be more damaging than high day temperatures [43]. High  
164 night temperatures can cause male sterility in cowpea [44]. The stage of floral bud development  
165 most sensitive to high temperatures occurs seven to nine days before anthesis, that is after  
166 meiosis, and involves premature degeneration of tapetal tissue and lack of endothelial  
167 development [45]. Transport of proline from anther walls to pollen is therefore inhibited in  
168 sensitive genotypes [46].

169 Cowpea is sensitive to photoperiod; thus, short day, day neutral and long-day types of cowpea  
170 exist [47]. Cowpea responses to photoperiod determine the time of first flowering and the length  
171 and effectiveness of the reproductive period [48].

172 Some cultivars have a quantitative response to photoperiod such that flowering is delayed by  
173 long days, while others are day-neutral in that the initiation of floral bud is not influenced by day  
174 length [37]. However, plant breeders have been successful in the development of photoperiod  
175 sensitive cultivars [49].

176 Cowpea grows well over a range of soils, from sands to heavy expandable clays but well drained  
177 soil is most preferred, as the crop cannot tolerate waterlogging [50]. Cowpea can be inter-  
178 cropped with maize, millet, sorghum, cassava or even rice in the traditional farming systems of  
179 the tropics. In such intercropping systems cowpea is often subjected to zero tillage practices  
180 developed mainly for the companion crop [51].



## 181 **Effects of moisture stress on cowpea and genetic variation in drought tolerance**

182 The effects of moisture stress on plant physiology differ with species and degree of tolerance as  
183 well as with the extent of the water deficit. Generally, moisture stress affects the process related  
184 to cell turgidity and particularly meristematic growth. If moisture stress continues, other  
185 physiological processes are affected. For instance, moisture stress changes stomatal opening  
186 leading to a reduction in photosynthetic rates and water transport through the xylem. This in turn  
187 causes reduced transport flux of absorbed nutrients by roots and in the whole plant [52]. This  
188 impedes phenological development leading to marked reduction in yield.

189 Several physiological processes, including osmotic adjustment and desiccation tolerance, have  
190 been suggested as contributing to adaptation to drought. Cowpea, however has displayed little  
191 osmotic adjustment in leaves [53]. Some genotypic differences have been reported in the ability  
192 of cowpea to survive imposed drought start of vegetative growth [54]. The ability of cowpea to  
193 survive vegetative stage drought is related to the sensitive responses of their stomata to soil water  
194 deficit [55] and maintenance of high leaf water potentials [56]. Studies have been conducted in  
195 which cowpea was subjected to drought during the vegetative stage and the reproductive stage,  
196 which showed that grain yield of cowpea is strongly dependent upon the water supply during the  
197 reproductive stage, with relatively little effect at the vegetative phase [56, 57]. However, further  
198 related studies have also shown that drought stress at the flowering or pod filling stages causes  
199 senescence and abscission of mature basal leaves. Akyeampong [58] and Gwathmey and Hall  
200 [59] reported that determinate cowpea that begins flowering early, but have delayed leaf  
201 senescence are able to recover after mid-season drought probably resulting from the maintenance  
202 of root viability, which could also enhance nitrogen fixation.

203 Early maturing varieties escape terminal drought [40] but if exposed to intermittent moisture  
204 stress during the vegetative growth stage, they perform very poorly [60]. Reductions in leaf area  
205 are responsible for drought induced reductions in seed yield of cowpea (Hall *et al.*, 1997;  
206 Summerfield and Roberts, 1985). Summerfield and Roberts [61] and Minchin and Summerfield  
207 [63] have argued that early maturity varieties depend more on drought escape mechanisms,  
208 which enables them to complete their life cycle before the incidence of terminal drought. If,  
209 however, they are exposed to erratic moisture stress during the vegetative or reproductive stages,  
210 they perform very poorly. Many aspects of plant growth are affected by drought stress [64],  
211 including leaf expansion, which is reduced due to the sensitivity of cell growth to water stress.  
212 Water stress also affects total leaf production, promotes senescence and abscission [65] resulting  
213 in decreased total leaf area per plant. Reduction in leaf area reduces crop growth and thus  
214 biomass production and seed yield is affected [58].

### 215 **Vegetative growth and water stress**

216 The vegetative part of the plant is made up of two main components: the mature leaves that  
217 function as a source of assimilates and the expanding leaves that act as a sink of assimilates in  
218 competition with reproductive organs and roots. In legumes, Ney and Wery [66] hypothesized  
219 that, in the absence of drought or heat stress, assimilates are specially translocated to vegetative  
220 sinks, thereby inducing abortion of flowers, until a sufficient amount of seeds reach the seed-  
221 filling stage. Seed growth then becomes the central sink and stimulates the terminate leaf  
222 appearance and abortion of the youngest seeds on the top of the plant [67]. Expanding leaves  
223 show a large range of size and age, from the last phytomer produced by the apical meristem of a  
224 shoot to the first visible leaf out of the apical bud.

225 Comprehensive descriptions of leaf and phytomer development were made in contrasting species  
226 for a large range of growing conditions including pea [68] cotton [69], white clover [70], and  
227 grapes [71]. An extended or more intense water deficit is required to obtain a significant  
228 reduction of vegetative sources because these same 10 leaves will become sources after a time-  
229 span of 10 phytochromes and may even not be all expanded if vegetative growth is stopped by  
230 reproductive sinks. For this reason and also because expanding leaves make a minor contribution  
231 to light interception compared with expanded leaves, the vegetative sources (represented, for  
232 example, by leaf area index) are given a lower sensitivity to water deficit than vegetative sinks.  
233 This effect has been detected in annual plants such as chickpea, cowpea, and cotton, it is more  
234 distinct in perennial plants such as white clover and vineyards [71, 72]. Among the processes  
235 involved in plant leaf area expansion, branching and leaf appearance on the main stem, the most  
236 and the least sensitive processes to water deficit, leaf expansion have an intermediate response to  
237 water stress [73].

### 238 **Variation in days to flowering, maturity and yield in cowpea**

239 One of the important agronomic traits in cowpea production is earliness which is measured by  
240 days to flowering and days to maturity. Many quantitative studies on the genetics of earliness  
241 parameters have showed high heritability estimates of 0.75 for days to flowering and 0.79 for  
242 days to pod maturity [74]. Hall and Patel [75] reported that early erect cowpea cultivars, which  
243 commence flowering about 30 days after sowing in the tropics, have proved to be useful in some  
244 dry environments because of their ability to escape drought. Also, Wien [76] reported that, the  
245 longer the reproductive period the larger the number of fruits that mature and the larger the yield.  
246 Genetic differences in the period of the reproductive period is related to growth habit.

## 247 **Drought tolerance mechanisms in cowpea**

248 Traditionally drought tolerance is defined as the ability of plants to live, grow and yield  
249 satisfactorily with limited soil water supply or under periodic water deficiencies [77]. Plants have  
250 established a number of elaborate molecular mechanisms to respond and adapt to various  
251 environmental stresses, including drought and high temperatures [78]. Batierno *et al.* [79]  
252 indicated that drought occurrence can be sporadic in the life cycle of crop plants. Bahar and  
253 Yildirim [80], also reported that, crops are highly vulnerable to damage due to limited water  
254 during flowering and pod setting stages. Selection of drought tolerant lines has been based on  
255 one of the mechanisms such as avoidance so that early maturing lines used as escape would have  
256 completed physiological maturity before the incidence of drought [9]. Studies on genetic  
257 variability and diversity in drought tolerance has been conducted to assist in the identification of  
258 suitable parents to improve cowpea for drought tolerance [81].

259 Numerous factors and mechanisms operate independently or jointly to enable plants cope with  
260 drought stress. Therefore, drought tolerance is manifested as a complex trait [82]. According to  
261 Mitra [83], the mechanisms that plants use to survive drought stress can be grouped into three  
262 categories. These include drought escape, drought avoidance and drought tolerance. Drought  
263 escape is defined as the ability of a plant to complete its life cycle before serious soil and plant  
264 water deficits occur. Drought avoidance is the ability of plants to sustain relatively high tissue  
265 water potential despite a shortage of soil moisture. Drought tolerance is the ability of plants to  
266 withstand water-deficit with low tissue water potential [19].

267 Crop plants therefore use more than one mechanism at a time to cope with drought. These  
268 mechanisms involve rapid phenological development (early flowering and early maturing),  
269 developmental plasticity (variation in duration of growth period depending on the extent of water

270 deficit) and remobilization of pre-anthesis assimilates. Plants develop strategies for maintaining  
271 turgor by increasing root depth or developing an efficient root system to maximize water uptake,  
272 and by reducing water loss through reduced epidermal, stomatal and lenticular conductance,  
273 reduced absorption of radiation by leaf rolling or folding and reduced evapo-transpiration surface  
274 [83]. According to Agbicodo *et al.* [84], the mechanisms of drought tolerance in cowpea are  
275 maintenance of turgor through osmotic adjustment (accumulation of solute in cell), increased cell  
276 elasticity and decreased cell size and desiccation tolerance by protoplast resistance. However, all  
277 these adaptation mechanisms of the plant to cope with drought have some disadvantages with  
278 respect to yield potential. For instance, a genotype with a shortened life cycle (drought escape)  
279 usually yields less compared to a genotype with a normal life cycle.

280 |  
281 The mechanisms that confer drought avoidance act by reducing water loss (such as stomatal  
282 closure and reduced leaf area) decrease carbon assimilation due to a reduction in physical  
283 transfer of carbon dioxide molecules, and increase leaf temperature thus reducing biochemical  
284 processes, which negatively affects yield. Plants try to maintain water content by accumulating  
285 various solutes that are nontoxic (such as frutans, trahalose, glycines betane, proline and  
286 polyamines) and do not interfere with plant processes and that are, therefore called compatible  
287 solutes [85]. However, many ions concentrated in the cytoplasm due to water loss are toxic to  
288 plants at high concentrations leading to what is termed a glassy state.

289 In this condition, whatever liquid is left in the cell has a high viscosity, increasing the chances of  
290 molecular interactions that can cause proteins to denature and membranes to fuse [86].  
291 Subsequently, crop adaption to water stress must reflect a balance among escape, avoidance and  
292 tolerance while maintaining adequate productivity. Though drought escape, avoidance, and

293 tolerance mechanisms have been described in cowpea [83], the drought response pathways  
294 associated with these mechanisms are not yet fully understood, and the degree to which these  
295 operate together or separately to allow the crop to cope with drought still needs to be established.

### 296 **Drought escape in cowpea**

297 The increased frequency of drought in some cowpea growing areas caused a shift to early  
298 maturing varieties [87]. Early maturing cowpea cultivars are desirable and have proven to be  
299 useful in some dry environments and years because of their ability to escape drought [74, 88].

300 Such early cultivars can reach maturity in as few as 60-70 days in many of the cowpea  
301 production zones of Africa. Earliness is important in Africa as early cultivars can provide food  
302 and marketable product available from the current growing season, and they can be grown in a  
303 diverse array of cropping systems. In addition to escaping drought, early maturing cultivars can  
304 escape some insect infestations [37]. Selection for early flowering and maturity and yield testing  
305 of breeding lines under water-stressed conditions has been used successfully in developing  
306 cowpea cultivars adapted to low rainfall areas [74]. Early maturing cowpea varieties that escape  
307 terminal drought have been released and widely accepted by African farmers. But, if exposed to  
308 recurrent drought during the vegetative or reproductive stages, these varieties perform very  
309 poorly. Efforts are therefore being made to breed cowpea varieties with enhanced drought  
310 tolerance for early, mid and terminal season drought stresses.

### 311 **Drought avoidance and tolerance in Cowpea**

312 In cowpea, two types of drought tolerance have been described at the seedling stage using the  
313 wooden box technique [60]. In experiments described by Mai-Kodomi *et al.* [89], all the  
314 seedlings of two susceptible lines TVu 7778 and TVu 8256, were completely dead 15 days after  
315 termination of watering. TVu 11979 stopped growth after the onset of drought stress but

316 exhibited a declining turgidity in all tissues of the plants including the unifoliate and the  
317 emerging tiny trifoliate for over two weeks. All plant parts such as the growing tip, unifoliate  
318 and epicotyls gradually died almost at the same time. Genotypes displaying this type of  
319 resistance mechanism were referred to as “Type 1” mode of resistance by Mai-Kodomi *et al.*  
320 [89]. In contrast, the “Type 2” drought tolerant lines like Dan Illa and Kanannado remained green  
321 for longer time and continued slow growth of the trifoliate under drought stress with varieties  
322 wilting and dying about four weeks after drought stress started. The two types of tolerance  
323 responses by cowpea seedlings to drought stress indicate that cowpea genotypes adopted  
324 different mechanisms to cope with prolonged drought encountered in the semi-arid regions of  
325 Africa where the crop is believed to have originated. Closure of stomata to reduce water loss  
326 through transpiration and cessation of growth (for type 1 drought avoidance) and osmotic  
327 adjustment and continued slow growth (drought tolerance in type 2) have been recommended as  
328 the possible mechanisms for drought tolerance in cowpea [22]. Cowpea is known as dehydration  
329 avoider with strong stomata sensitivity and reduced growth rate [22]. This seems to be the  
330 mechanism underlying the Type 1 reaction to drought of Tvu 11986 and Tvu 11979.

331 The type 2 reaction of Dan Illa and Kanannado appears to be a mixture of three mechanisms:  
332 stomata regulation (partial opening), osmotic control and selective mobilization with distinct  
333 visible differences in the desiccation of lower leaves compared to the upper leaves and growing  
334 tips [60]. It seems that the type 2 mechanism of drought tolerance is more effective in keeping  
335 the plants alive for a longer time and ensures better chances of recovery than type 1 when the  
336 drought spell ends. Both drought tolerant lines Dan Illa and Kanannado are local varieties  
337 commonly grown in the Sudano-Sahelian border areas of Nigeria and Niger Republic, indicating  
338 that in these areas farmers have selected cowpea varieties with good adaptation to drought.

339 Similarly, Muchero *et al.* [90] studied 14 genotypes of cowpea at seedling stage and established  
340 the presence of significant genetic variation in responses to drought stress. Genotypes, IT93 K-  
341 503-1 and IT98 K-499-39 were consistently more tolerant whereas CB46 and Bambeay 21 were  
342 more susceptible.

343 Drought-tolerant genotypes, once identified, will open new avenues for indirect selection, either  
344 by analysis of their physiological properties [91] and/or by identifying DNA markers for these  
345 traits [92]. Several other mechanisms may partially explain the extreme dehydration avoidance  
346 of cowpea. The mechanisms through which cowpea is able to resist vegetative-stage drought  
347 may be related to the limited decrease of leaf water potential even under extreme drought. The  
348 lowest leaf water potential recorded for cowpea is -18 bars (-1.8 Mpa) [93, 94], whereas peanut  
349 has developed leaf water potentials under drought as low as -82 bars (-8.2 Mpa) [95]. Cowpea  
350 also changes the position of leaflets under drought (a drought avoidance mechanism).  
351 They become paraheliotropic and oriented parallel to the sun's rays when subjected to soil  
352 drought, causing them to be cooler and thus transpire less [96], which helps to minimize water  
353 loss and maintain water potential.

#### 354 **Transpiration rate**

355 Transpiration rate per unit of leaf area can be measured with similar equipment as for Net carbon  
356 exchange rate (NCER) or can be indirectly assessed with stomatal conductance measurements  
357 using a porometer in pea [68]. In field conditions, especially at early stages of the plant life,  
358 when plant canopy is not full established, the significance of this measurement for crop water  
359 consumption is restricted by the importance of water evaporation from the soil surface receiving  
360 solar radiation. Despite this limit, Lacape *et al.* [97] obtained, in cotton crops, similar  
361 relationships of soil drying Fraction of Transpired Soil Water (FTSW)) with stomatal



362 conductance and with daily crop water up take by plants measured with a neutron probe and  
363 water balance. Similar results were obtained in pea when comparing stomatal conductance and  
364 transpiration measured in pots [98].

### 365 **Biomass yield and nitrogen fixation**

366 Among the performance criteria of the crop system, biomass production is undoubtedly the most  
367 sensitive to soil water deficit. In a number of experiments in various crop species, even with  
368 short and moderate water deficit, a reduction in above-ground vegetative biomass has been  
369 observed [69, 70, 99]. In each of these cases, the major effect of water deficit is probably a sink  
370 limitation of biomass production, as expansion of all the phytomers in development in the apical  
371 bud is irreversibly reduced, while photosynthesis of mature leaves is maintained, or is less  
372 affected during the stress, and restored to the level of the control after the period of water deficit  
373 [67, 100]. Only when the intensity and/or duration of water deficit are sufficient, does the source  
374 limitation become dominant, as photosynthesis and light interception are reduced (by cessation  
375 of branching and development of leaves out of the shoot tips; Belaygue *et al.* [73]. This may  
376 explain why current crop models, which are based on source limitation of biomass by water  
377 deficit [101], may fail in reproducing the effects of short and moderate soil water deficit on  
378 biomass and grain yield. The amount of nitrogen fixed, an important criterion of legume  
379 performance in low-input systems, has sensitivity to water deficit that is equal to or even higher  
380 than biomass production as it is the result of a reduction in both the biomass and the percentage  
381 of nitrogen derived from the atmosphere [102].

### 382 **Duration of flowering**

383 Date of flowering is mainly controlled by temperature and photoperiod and is therefore only  
384 affected by water deficit through increased canopy temperature was linked to stomatal closure in

385 cotton [97]. In indeterminate plants the duration of the flowering period is generally reduced by  
386 water deficit or moderate heat stress, although a severe but short heat stress inducing flower  
387 abortion may increase it, as long as the plant has the ability to recover from the stress [103]. In  
388 field conditions, especially in tropical regions, water deficit and heat stress are frequently  
389 occurring simultaneously and their effects on the reduction of flowering duration are additive. As  
390 shown in cotton and pea, this shortening of the reproductive period by water deficit can be  
391 analysed as the result of a higher sensitivity of phytomer appearance compared with flower  
392 production, thereby reducing the number of nodes above the last mature leaf and accelerating the  
393 cut-out [97].

#### 394 **Grain yield and harvest index**

395 The importance of maintenance of reproductive development compared with vegetative growth  
396 is that harvest index is less affected by water deficit than above-ground biomass, except for  
397 severe water deficit occurring after cut out [97]. Similar observations have been made in lupins  
398 [104] although attributed to hastening of the reproductive development after a transient water  
399 deficit. When soil dehydration occurs after the start of flowering and is sufficient to reduce  
400 vegetative sinks (by cessation of branching and reduction of leaf expansion) without reducing  
401 light interception (if LAI is already higher than 3) and photosynthesis, grain yield can even be  
402 increased by this water deficit, leading to an increase in harvest index [104]. At the same time,  
403 the reduction in plant transpiration may be sufficient to induce a significant saving in water and  
404 an increase in water-use efficiency for grain production. This suggests that transpiration is  
405 reduced in the same proportion as biomass yield, but grain yield can be increased by water stress  
406 as long as biomass dry matter is not reduced by 40–50% [105, 106].

## 407 **Screening approaches for drought tolerance**

408 Two main approaches have been so far used for screening and breeding for drought tolerance in  
409 plants. The first is the performance approach that utilizes grain yield and its components as the  
410 main criteria, since yield is the integrated expression of the entire array of traits related to  
411 productivity under stress [107]. This approach focuses on empirical validation of the yield of  
412 varieties over several years and locations in areas with known drought incidence patterns using  
413 standard field designs. Significant achievements have been made in developing cowpea varieties  
414 with better adaptation to water stress [107, 108, 74, 94]. Though various cowpea breeding  
415 materials such as F<sub>2</sub>, F<sub>3</sub> and backcross populations have been used for drought tolerance studies  
416 in cowpea, the empirical approach mainly relies on the use of recombinant inbred lines (RIL) to  
417 enable the consistent evaluation of performance and understanding of genotype-by-environment  
418 interaction, as the intensity and frequency of naturally occurring drought stress are not entirely  
419 predictable. The RIL population, developed through single seed descent of several selfed  
420 generations consists of individual lines carrying dispersed homozygous segments of a parental  
421 chromosome.

422 The second approach employs analyses of physiological or morphological traits that contribute  
423 significantly to growth and yield in the event of drought. These traits include delayed leaf  
424 senescence, water-use efficiency, water potential, relative turgidity, leaf gas exchange, relative  
425 water content, diffusion pressure deficit, chlorophyll stability index, and carbon isotope  
426 discrimination—[109, 110, 35, 55]. For most of these traits, there have been conflicting results on  
427 their value in selecting for tolerant varieties in the field [111, 112]. Significant contributions of  
428 these physiological traits were found typically under extreme water deficit conditions where  
429 plant survival rather than yield is the key character of interest [113]. Such extreme conditions are

430 not typically encountered in cowpea production zones of West Africa. Based on the available  
431 evidence, it will be sensible to analyse the inherent differences in sensitivity to drought in  
432 cowpea by direct assessment of growth and yield components in the field under typical  
433 production conditions. Slabbert *et al.* [114] noted that whenever the physiological approach is  
434 used in selecting varieties, their performance should be validated in the field under naturally  
435 occurring drought. Agbicodo *et al.* [84] based on a review of several studies identified the  
436 following traits as the more reliable in developing cowpea cultivars with tolerance to drought.  
437 These include determination of chlorophyll fluorescence, stomatal conductance measurements,  
438 abscisic acid measurements, measuring free proline levels, wooden box screening for drought  
439 tolerance at the seedling stage, and delayed leaf senescence.

440 In the evaluation of several cowpea lines, Muchero *et al.* [90] identified IT93K503-1 as the most  
441 tolerant to drought. Subsequently, highly reproducible quantitative trait locus (QTL) for this trait  
442 were mapped in a cowpea recombinant inbred line (RIL) population 'IT93K503-1 x CB46' in  
443 which 10 QTL regions, *Dro-1* to *Dro-10*, were identified on a genetic linkage map using both  
444 screen-house and field-based phenotyping [115].

#### 445 **Effects of water stress on grain nutrient content and phytochemical variability in** 446 **cowpea seeds under contrasting moisture conditions**

447 Pulses are a vital source of plant-based proteins and amino acids for people around the globe and  
448 may be eaten as part of a healthy diet to address obesity, as well as to prevent and help manage  
449 chronic diseases such as diabetes, coronary conditions and cancer; they are also an important  
450 source of plant-based protein for animals [116, 5]. In a study of the phenolic content and  
451 antioxidant properties of selected cowpea varieties tested in bovine peripheral blood. Adjei-  
452 Fremah *et al.* (2015) reported that, the potential of cowpea polyphenols to reduce oxidative stress

453 in livestock production is high which is a positive indication for human health improvement.  
454 Viets [118] and Alam [119] reported that, drought reduces both nutrient uptake by the roots and  
455 transport from the roots to the shoots, because of restricted transpiration rates and impaired  
456 active transport and membrane permeability, the decline in soil moisture also results in a  
457 decrease in the diffusion rate of nutrients in the soil to the absorbing root surface [120, 121]. This  
458 will consequently affect the seed yield and the nutritive value of the seed. A study conducted in  
459 Pakistan by [5] on the antioxidant activity of the extracts of some cowpea cultivars commonly  
460 consumed in Pakistan, revealed that, phenolic constituents contained in cowpea may have a  
461 future role as ingredients in the development of functional foods to determine the antioxidant  
462 benefits of the cowpea consumed. The assessment of antioxidant potential might be a fruitful  
463 approach for advocating them as nutraceuticals, in addition to them being potential protein and  
464 carbohydrate sources. The consumption of a processed cowpea would not only improve nutrient  
465 utilization, but also provide potential nutraceuticals for human health. It could therefore be  
466 concluded that cowpea could contribute significantly in the management and/or prevention of  
467 degenerative diseases associated with free radical damage, in addition to their traditional role of  
468 preventing protein malnutrition. Therefore, it will be of immense value to determine the  
469 antioxidant, phenolic and other nutritional values of cowpea under contrasting moisture regimes  
470 for developed cowpea inbred lines in this study.

#### 471 **Genotype by environment (G x E) interaction**

472 Genotype by environment interaction (G x E) can be defined as the differential response of  
473 varying genotypes under change(s) in the environment [122]. The ability, or inability, of  
474 organisms to adapt to changes in their environment at the speed necessary, determines the  
475 continuation, extinction, or evolution of species [123]. Genotype by environmental interaction is

476 an important factor affecting the breeding and stability of improved and elite genotypes  
477 developed through plant improvement programmes in both the developed and developing  
478 countries [124] including Ghana. A plant cannot migrate when challenged by fluctuations in  
479 environmental conditions, which means that it has to cope with environmental heterogeneity by  
480 adapting to the new or fluctuating environment [125]. It can do so via changing the phenotypic  
481 expression, a phenomenon called 'phenotypic plasticity', which is often involves altering gene  
482 expression and plant physiology in response to environmental signals [126–128]. Scheiner [129],  
483 reported that it is not only phenotypic plasticity trait and developmental stage specific but it also  
484 often depends on the genotype. When phenotypic plasticity differs between genotypes, this is  
485 described as genotype by environment interaction. Dean [130], reported that environmental  
486 factors such as temperature, light intensity, and humidity, are the major cause of genotypic and  
487 phenotypic variation. Lande and Shannon [131] reported that genotype by environment  
488 interaction has heavy implications on the evolution of species, they further on suggest that in  
489 constant or unpredictable environments, genetic variance reduces population mean fitness and  
490 increases the risk of extinction. Although the importance of the differential effect of the  
491 environment on different plant genotypes has been known for a long time and has been  
492 considered in crop-breeding programs, it is generally viewed as a thought-provoking issue. When  
493 phenotypic plasticity differs between genotypes, this is described as Genotype by environment  
494 interaction. Gerrano *et al.* [132], defined an "ideal" test environment, which is a virtual  
495 environment that has the longest vector of all test environments (most discriminating) and is  
496 located on the AEC abscissa (most representative). Yan *et al.* [133] reported that G and GE must  
497 be considered simultaneously in mega-environment analysis, genotype evaluation, and test-  
498 environment evaluation; separation of G from GE is primarily a mathematical manipulation that

499 is not always supported by biological evidence combining G and GE in GGE biplot analysis is  
500 essential for addressing plant breeding and agricultural problems. The performance of a genotype  
501 is determined by three factors: genotypic main effect (G), environmental main effect (E) and  
502 their interaction [134]. Lin and Binns [135] introduced a new stability concept as yearly variance  
503 within test locations (YV) which relates to stability in time (across years). Also, Lin and Binns  
504 [136] defined the superiority index (PI) as the genotype general superiority and defined it as the  
505 distance mean square between the genotype's response and the maximum response over  
506 environments. Multi-locational trials are necessary in order to confirm the distinctiveness,  
507 uniformity and stability of newly developed crop varieties in readiness for recommendation to  
508 farmers [137]. Understanding of the genetic variability of cowpea is important to design and  
509 accelerate conventional breeding programmes [132]. Collection, characterization and evaluation  
510 of available cowpea germplasm, quantification of the magnitude of diversity and classification  
511 into groups facilitate identification of genetic variability that enables breeders to select traits of  
512 interest for an improvement programme [138, 139]. Therefore, variety trials in a breeding  
513 program are usually conducted in several environments, to minimize the risk of discarding  
514 genotypes that potentially perform well in some, but not in all, environments; that is, when there  
515 is significant  $G \times E$  and, in particular, when cross-over interaction occurs [140].

#### 516 **Farmer preferences, production constraints and perception on drought in cowpea**

517 For cowpea varieties with improved tolerance to drought to be accepted by farmers, it is  
518 important to solicit their views and get them involved right from the beginning of the research  
519 and breeding process to the end to help facilitate their adoption [141]. A major factor that affects  
520 production and consumption of cowpea in Ghana is varietal preference [3]. Ghanaians are known  
521 to have a high preference for cream seeded cowpea [29].

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

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



## 545 **Markers in cowpea Breeding**

546 Modern technologies, such as marker-assisted selection (MAS), in combination with  
547 conventional breeding have been successfully used for genetic enhancement of other crop  
548 species. The development and use of biochemical-based analytical techniques and molecular  
549 marker technologies, such as restriction fragment length polymorphisms (RFLPs), random  
550 amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs),  
551 and microsatellites or simple sequence repeats (SSRs), have greatly facilitated the analysis of the  
552 structure of plant genomes and their evolution, including relationships among the Leguminoseae  
553 [1, 133, 133, 149]. This in turn has contributed significantly to our current understanding of the  
554 cowpea genome organization and evolution. There is a clear need for leveraging modern  
555 biotechnological tools to complement conventional breeding in cowpea. Such efforts should  
556 focus on the development of molecular markers and protocols for use in marker-assisted  
557 selection (MAS) and marker-assisted breeding. [149]. Recently, a Dehydration-Responsive  
558 Element-Binding protein2A (DREB2A) ortholog was isolated from cowpea, VuDREB2A  
559 (GenBank: JN629045.3) which was highly induced in response to desiccation, heat and salinity,  
560 and conferred enhanced drought tolerance by up regulation of several stress-responsive genes in  
561 transgenic Arabidopsis [78]. A Ser/Thr-rich region immediately downstream to the DNA binding  
562 domain in VuDREB2A appeared to have some role in the stability of the protein, since its  
563 removal led to a dwarf phenotype and enhanced expression of some of the downstream genes of  
564 VuDREB2A, similar to DREB2A CA [150]. This provides vital clue to the possibilities of  
565 existence of similar pathways regulating VuDREB2A in cowpea. A thorough understanding of  
566 the molecular mechanisms underlying the stress responses of crop plants, especially tolerant

567 species such as cowpea is necessary for development of enhanced stress-tolerant varieties for  
568 sustainable agriculture in the future

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### 573 **Conclusion**

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

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