

Review Paper

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” singly 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.](#) cowpea, drought, phenology, markers and
32 | participatory rural appraisal

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36 | **Introduction**

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

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

51 |
52 | In many parts of West Africa, cowpea hay is also critical in the feeding of animals during the dry
53 | season, in addition, cowpea is a nitrogen-fixing plant, when used in rotation with cereal crops it

54 can help restore soil fertility. Therefore, cowpea can play an important role in the development
55 of agriculture [6].

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

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

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

76 | A study which also utilized over 10,000 accessions of world collection at the International
77 | Institute of Tropical Agriculture (IITA) discovered that the collection from West Africa spread to
78 | India by 2000 BC[11]. It was introduced into Europe by the Greeks and Romans who grew it
79 | under the name Phaseolus. It was introduced into the Americas relatively more recently. The
80 | research work carried out by IITA showed that germplasm accessions from West Africa showed
81 | greater diversity than those from East Africa [11]. These studies provided further evidence that
82 | West Africa was the primary centre of domestication. The centre of maximum diversity of
83 | cultivated cowpea is found in West Africa, encompassing the Savanna regions of Nigeria,
84 | southern Benin, Togo, and north-west part of Cameroon [7]. Verdcourt [12] reported that *Vigna*
85 | has several species, but the exact number varies according to different authors.

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

92 | The cultivar group *unguiculata* is the most diverse of the four and is widely grown in Africa,
93 | Asia and Latin America (Fang *et al.*, 2007).—Subspecies *unguiculata* is the only cultivated
94 | cowpea, while the other three are wild relatives. Several studies have shown that cowpea was
95 | probably domesticated by African farmers [14] and assumed to have evolved in Africa, because
96 | wild cowpeas only exist in Africa and Madagascar [15]. Although the centre of diversity of wild
97 | *Vigna* species is in south-eastern Africa, West Africa is a major centre of diversity of cultivated
98 | cowpea [11]. Coulibaly and Lowenberg-De Boer [16] used data from amplified fragment length

99 polymorphism (AFLP) marker analyses of cowpea accessions to hypothesize that cowpea
100 domestication occurred in north-eastern Africa and could have occurred at the same time with
101 the domestication of sorghum and pearl millet in the third millennium B.C. [15].

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

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

109 **Plant characteristics**

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

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122 in Nigeria is due to their ease of dehulling and greater expansion capacity. Grain coat colour is
123 also considered as one of the useful phenotypic markers in cowpea breeding due to its stable
124 expression and suitability for observation [23].

125 **Cowpea production and distribution**

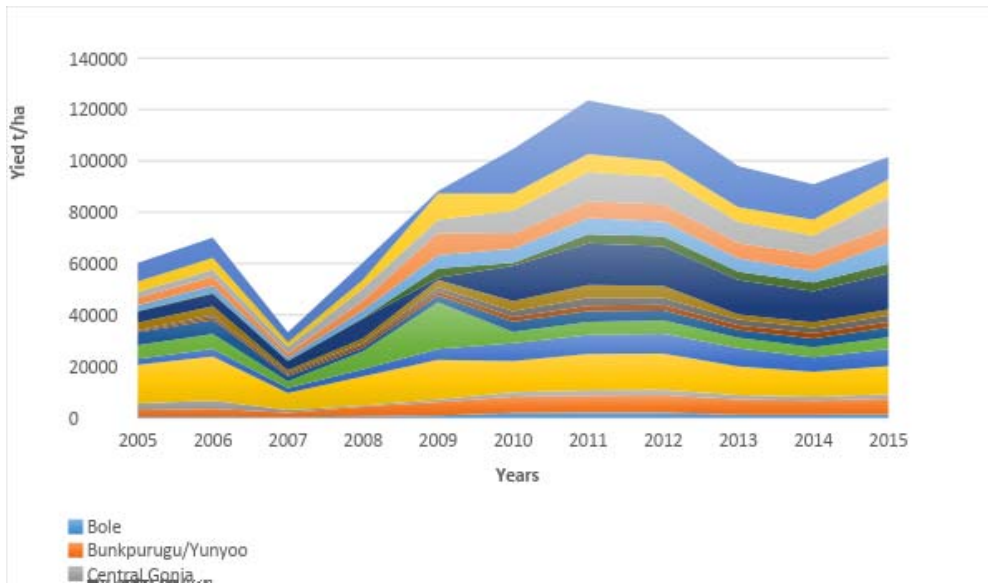
126 Cowpea is cultivated throughout the African continent as well as in some parts of South East
127 Asia and Latin America. Though native to West Africa, this legume has become a part of the diet
128 of about 110 million people [24]. In West Africa, cowpea has become an integral part of the
129 farming systems [24]. Cowpea production in the world—was estimated at 12.5 million hectares,
130 with an annual output of more than 3 million tons [25]. Africa alone produces about 83% of the
131 world output. Nigeria is the largest world's producer (45.76%), followed by Niger (15%), Brazil
132 (12%), and 5 % for Burkina Faso [26], with Africa's arid Sahel region accounting for 64%. In
133 Ghana, cowpea cultivation is primarily done in the northern and upper West regions. Cowpea
134 commercial regions include the Upper East, Brong Ahafo, Eastern, Volta and Ashanti. The
135 Ghana government policy objective for the cowpea subsector is to encourage increased
136 production so that self-reliance and food security can be achieved. Yet, the production of the
137 crop has fluctuated over the years partly due to climatic conditions and policy issues [27].
138 Average yield of cowpea in Ghana is 1,3 t/ha with a potential estimated at 1.96 t/ha [28].

139 Cowpea farming serves as a vital component of sustainable cropping system in Ghana because of
140 its nitrogen fixing ability and socio-cultural values [29]. The crop is considered drought and heat
141 tolerant, and is able to fix—nitrogen up to 240 t/ha and leaving—about 60–70 kg nitrogen for the
142 following crops [30]. Production is mainly done by small-scale resource-poor farmers practicing
143 mostly peasant agriculture and growing largely unimproved varieties resulting in low output.
144 SARI [31] carried out studies, which showed an adoption rate per annum of 3.9 % for improved

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145 varieties in northern Ghana, confirming that majority of farmers still grow landraces or
146 unimproved varieties of the crop.



147

148 Fig._1: A graph showing trend of Cowpea production in Northern Ghana- (MOFA-SRID, 2016)

149

150 Climate and soil requirements for cowpea production

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

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160 temperatures accelerating crop development, high temperatures also allow little time for carbon
161 assimilation that could be partitioned to the grain and substantially reduces yield [39]. Singh [40]
162 reported that flower and pod shedding also increase at temperatures above 35°C leading to a
163 marked reduction in yield. Cowpea requires a rainfall of 600 to 800 mm per annum for optimum
164 growth and development. Medium and long duration types require a rainfall between 600 and
165 1500 mm per annum [41]. Excessive rain or atmospheric humidity results in reduction in yield
166 due to a high incidence of fungal diseases [42].

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

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

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

180 | Cowpea grows well over a range of soils, from sands to heavy expandable clays but well drained
181 soil is most preferred, as the crop cannot tolerate waterlogging [50]. Cowpea can be inter-
182 cropped with maize, millet, sorghum, cassava or even rice in the traditional farming systems of

183 the tropics. In such intercropping systems cowpea is often subjected to zero tillage practices
184 developed mainly for the companion crop [51].

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

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

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

205 | have delayed leaf senescence are able to recover after mid-season—drought probably resulting
206 | from the maintenance of root viability, which could also enhance nitrogen fixation.

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

219 | **Vegetative growth and water stress**

220 | The vegetative part of the plant is made up of two main components: the mature leaves that
221 | function as a source of assimilates and the expanding leaves that act as a sink of assimilates in
222 | competition with reproductive organs and roots. In legumes, Ney and Wery [66]—hypothesized
223 | that, in the absence of drought or heat stress, assimilates are specially translocated to vegetative
224 | sinks, thereby inducing abortion of flowers, until a sufficient amount of seeds reach the seed-
225 | filling stage. Seed growth then becomes the central sink and stimulates the—terminate leaf
226 | appearance and abortion of the youngest seeds on the top of the plant [67]. Expanding leaves

227 show a large range of size and age, from the last phytomer produced by the apical meristem of a
228 shoot to the first visible leaf out of the apical bud.

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

242 **Variation in days to flowering, maturity and yield in cowpea**

243 One of the important agronomic traits in cowpea production is earliness which is measured by
244 days to flowering and days to maturity. Many quantitative studies on the genetics of earliness
245 parameters have showed high heritability estimates of 0.75 for days to flowering and 0.79 for
246 days to pod maturity [74]. Hall and Patel [75] reported that early erect cowpea cultivars, which
247 commence flowering about 30 days after sowing in the tropics, have proved to be useful in some
248 dry environments because of their ability to escape drought. Also, Wien [76] reported that, the

249 longer the reproductive period the larger the number of fruits that mature and the larger the yield.

250 Genetic differences in the period of the reproductive period is related to growth habit.

251 **Drought tolerance mechanisms in cowpea**

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

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

271 Crop plants therefore use more than one mechanism at a time to cope with drought. These
272 mechanisms involve rapid phenological development (early flowering and early maturing),
273 developmental plasticity (variation in duration of growth period depending on the extent of water
274 deficit) and remobilization of pre-anthesis assimilates. Plants develop strategies for maintaining
275 turgor by increasing root depth or developing an efficient root system to maximize water uptake,
276 and by reducing water loss through reduced epidermal, stomatal and lenticular conductance,
277 reduced absorption of radiation by leaf rolling or folding and reduced evapo-transpiration surface
278 [83]. According to Agbicodo *et al.* [84], the mechanisms of drought tolerance in cowpea are
279 maintenance of turgor through osmotic adjustment (accumulation of solute in cell), increased cell
280 elasticity and decreased cell size and desiccation tolerance by protoplast resistance. However, all
281 these adaptation mechanisms of the plant to cope with drought have some disadvantages with
282 respect to yield potential. For instance, a genotype with a shortened life cycle (drought escape)
283 usually yields less compared to a genotype with a normal life cycle.

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

293

294 | In this condition, whatever liquid is left in the cell has a high viscosity, increasing the chances of
295 | molecular interactions that can cause proteins to denature and membranes to fuse [86].
296 | Subsequently, crop adaption to water stress must reflect a balance among escape, avoidance and
297 | tolerance while maintaining adequate productivity. Though drought escape, avoidance, and
298 | tolerance mechanisms have been described in cowpea [83], the drought response pathways
299 | associated with these mechanisms are not yet fully understood, and the degree to which these
300 | operate together or separately to allow the crop to cope with drought still needs to be established.

301 | **Drought escape in cowpea**

302 | The increased frequency of drought in some cowpea growing areas caused a shift to early
303 | maturing varieties [87]. Early maturing cowpea cultivars are desirable and have proven to be
304 | useful in some dry environments and years because of their ability to escape drought [74, 88].
305 | Such early cultivars can reach maturity in as few as 60-70 days in many of the cowpea
306 | production zones of Africa. Earliness is important in Africa as early cultivars can provide food
307 | and marketable product available from the current growing season, and they can be grown in a
308 | diverse array of cropping systems. In addition to escaping drought, early maturing cultivars can
309 | escape some insect infestations [37]. Selection for early flowering and maturity and yield testing
310 | of breeding lines under water-stressed conditions has been used successfully in developing
311 | cowpea cultivars adapted to low rainfall areas [74]. Early maturing cowpea varieties that escape
312 | terminal drought have been released and widely accepted by African farmers. But, if exposed to
313 | recurrent drought during the vegetative or reproductive stages, these varieties perform very
314 | poorly. Efforts are therefore being made to breed cowpea varieties with enhanced drought
315 | tolerance for early, mid and terminal season drought stresses.

316 | **Drought avoidance and tolerance in Cowpea**

317 In cowpea, two types of drought tolerance have been described at the seedling stage using the
318 wooden box technique [60]. In experiments described by Mai-Kodomi *et al.* [89], all the
319 seedlings of two susceptible lines TVu 7778 and TVu 8256, were completely dead 15 days after
320 termination of watering. TVu 11979 stopped growth after the onset of drought stress but
321 exhibited a declining turgidity in all tissues of the plants including the unifoliate and the
322 emerging tiny trifoliates for over two weeks. All plant parts such as the growing tip, unifoliates
323 and epicotyls gradually died almost at the same time. Genotypes displaying this type of
324 resistance mechanism were referred to as “Type 1” mode of resistance by Mai-Kodomi *et al.*
325 [89]. In contrast, the “Type 2” drought tolerant lines like Dan Ila and Kanannado remained green
326 for longer time and continued slow growth of the trifoliates under drought stress with varieties
327 wilting and dying about four weeks after drought stress started. The two types of tolerance
328 responses by cowpea seedlings to drought stress indicate that cowpea genotypes adopted
329 different mechanisms to cope with prolonged drought encountered in the semi-arid regions of
330 Africa where the crop is believed to have originated. Closure of stomata to reduce water loss
331 through transpiration and cessation of growth (for type 1 drought avoidance) and osmotic
332 adjustment and continued slow growth (drought tolerance in type 2) have been recommended as
333 the possible mechanisms for drought tolerance in cowpea [22]. Cowpea is known as dehydration
334 avoider with strong stomata sensitivity and reduced growth rate [22]. This seems to be the
335 mechanism underlying the Type 1 reaction to drought of Tvu 11986 and Tvu 11979.

336 |
337 The type 2 reaction of Dan Ila and Kanannado appears to be a mixture of three mechanisms:
338 stomata regulation (partial opening), osmotic control and selective mobilization with distinct

339 visible differences in the desiccation of lower leaves compared to the upper leaves and growing
340 tips [60]. It seems that the type 2 mechanism of drought tolerance is more effective in keeping
341 the plants alive for a longer time and ensures better chances of recovery than type 1 when the
342 drought spell ends. Both drought tolerant lines Dan Illa and Kanannado are local varieties
343 commonly grown in the Sudano-Sahelian border areas of Nigeria and Niger Republic, indicating
344 that in these areas farmers have selected cowpea varieties with good adaptation to drought.
345 Similarly, Muchero *et al.* [90] studied 14 genotypes of cowpea at seedling stage and established
346 the presence of significant genetic variation in responses to drought stress. Genotypes, IT93 K-
347 503-1 and IT98 K-499-39 were consistently more tolerant whereas CB46 and Bambey 21 were
348 more susceptible.

349
350 Drought-tolerant genotypes, once identified, will open new avenues for indirect selection, either
351 by analysis of their physiological properties [91] and/or by identifying DNA markers for these
352 traits [92]. Several other mechanisms may partially explain the extreme dehydration avoidance
353 of cowpea. The mechanisms through which cowpea is able to resist vegetative-stage drought
354 may be related to the limited decrease of leaf water potential even under extreme drought. The
355 lowest leaf water potential recorded for cowpea is -18 bars (-1.8 Mpa) [93, 94], whereas peanut
356 has developed leaf water potentials under drought as low as -82 bars (-8.2 Mpa) [95]. Cowpea
357 also changes the position of leaflets under drought (a drought avoidance mechanism).

358 They become paraheliotropic and oriented parallel to the sun's rays when subjected to soil
359 drought, causing them to be cooler and thus transpire less [96], which helps to minimize water
360 loss and maintain water potential.

361

362 | **Transpiration rate**

363 | Transpiration rate per unit of leaf area can be measured with similar equipment as for Net carbon
364 | exchange rate (NCER) or can be indirectly assessed with stomatal conductance measurements
365 | using a porometer in pea [68]. In field conditions, especially at early stages of the plant life,
366 | when plant canopy is not full established, the significance of this measurement for crop water
367 | consumption is restricted by the importance of water evaporation from the soil surface receiving
368 | solar radiation. Despite this limit, Lacape *et al.* [97] obtained, in cotton crops, similar
369 | relationships of soil drying Fraction of Transpired Soil Water (FTSW)) with stomatal
370 | conductance and with daily crop water up take by plants measured with a neutron probe and
371 | water balance. Similar results were obtained in pea when comparing stomatal conductance and
372 | transpiration measured in pots [98].

373 | **Biomass yield and nitrogen fixation**

374 | Among the performance criteria of the crop system, biomass production is undoubtedly the most
375 | sensitive to soil water deficit. In a number of experiments in various crop species, even with
376 | short and moderate water deficit, a reduction in above-ground vegetative biomass has been
377 | observed [69, 70, 99].—In each of these cases, the major effect of water deficit is probably a sink
378 | limitation of biomass production, as expansion of all the phytomers in development in the apical
379 | bud is irreversibly reduced, while photosynthesis of mature leaves is maintained, or is less
380 | affected during the stress, and restored to the level of the control after the period of water deficit
381 | [67, 100]. Only when the intensity and/or duration of water deficit are sufficient, does the source
382 | limitation become dominant, as photosynthesis and light interception are reduced (by cessation
383 | of branching and development of leaves out of the shoot tips; Belaygue *et al.* [73]. This may
384 | explain why current crop models, which are based on source limitation of biomass by water

385 deficit [101], may fail in reproducing the effects of short and moderate soil water deficit on
386 biomass and grain yield. The amount of nitrogen fixed, an important criterion of legume
387 performance in low-input systems, has sensitivity to water deficit that is equal to or even higher
388 than biomass production as it is the result of a reduction in both the biomass and the percentage
389 of nitrogen derived from the atmosphere [102].

390 **Duration of flowering**

391 Date of flowering is mainly controlled by temperature and photoperiod and is therefore only
392 affected by water deficit through increased canopy temperature was linked to stomatal closure in
393 cotton [97]. In indeterminate plants the duration of the flowering period is generally reduced by
394 water deficit or moderate heat stress, although a severe but short heat stress inducing flower
395 abortion may increase it, as long as the plant has the ability to recover from the stress [103]. In
396 field conditions, especially in tropical regions, water deficit and heat stress are frequently
397 occurring simultaneously and their effects on the reduction of flowering duration are additive. As
398 shown in cotton and pea, this shortening of the reproductive period by water deficit can be
399 analysed as the result of a higher sensitivity of phytomer appearance compared with flower
400 production, thereby reducing the number of nodes above the last mature leaf and accelerating the
401 cut-out [97].

402 **Grain yield and harvest index**

403 The importance—of—maintenance of reproductive development compared with vegetative
404 growth is that harvest index is less affected by water deficit than above-ground biomass, except
405 for severe water deficit occurring after cut out [97]. Similar observations have been made in
406 lupins [104] although attributed to an hastening of the reproductive development after a transient
407 water deficit. When soil dehydration occurs after the start of flowering and is sufficient to reduce

408 vegetative sinks (by cessation of branching and reduction of leaf expansion) without reducing
409 light interception (if LAI is already higher than 3) and photosynthesis, grain yield can even be
410 increased by this water deficit, leading to an increase in harvest index [104]. At the same time,
411 the reduction in plant transpiration may be sufficient to induce a significant saving in water and
412 an increase in water-use efficiency for grain production. This suggests that transpiration is
413 reduced in the same proportion as biomass yield, but grain yield can be increased by water stress
414 as long as biomass dry matter is not reduced by 40–50% [105, 106].

415 **Screening approaches for drought tolerance**

416 Two main approaches have been so far used for screening and breeding for drought tolerance in
417 plants. The first is the performance approach that utilizes grain yield and its components as the
418 main criteria, since yield is the integrated expression of the entire array of traits related to
419 productivity under stress [107].—This approach focuses on empirical validation of the yield of
420 varieties over several years and locations in areas with known drought incidence patterns using
421 standard field designs. Significant achievements have been made in developing cowpea varieties
422 with better adaptation to water stress [107, 108, 74, 94]. Though various cowpea breeding
423 materials such as F₂, F₃ and backcross populations have been used for drought tolerance studies
424 in cowpea, the empirical approach mainly relies on the use of recombinant inbred lines (RIL) to
425 enable the consistent evaluation of performance and understanding of genotype-by-environment
426 interaction, as the intensity and frequency of naturally occurring drought stress are not entirely
427 predictable. The RIL population, developed through single seed descent of several selfed
428 generations consists of individual lines carrying dispersed homozygous segments of a parental
429 chromosome.

430 | The second approach employs analyses of physiological or morphological traits that contribute
431 | significantly to growth and yield in the event of drought. These traits include delayed leaf
432 | senescence, water-use efficiency, water potential, relative turgidity, leaf gas exchange, relative
433 | water content, diffusion pressure deficit, chlorophyll stability index, and carbon isotope
434 | discrimination [109, 110, 35, 55]. For most of these traits, there have been conflicting results on
435 | their value in selecting for tolerant varieties in the field [111, 112]. Significant contributions of
436 | these physiological traits were found typically under extreme water deficit conditions where
437 | plant survival rather than yield is the key character of interest [113]. Such extreme conditions are
438 | not typically encountered in cowpea production zones of West Africa. Based on the available
439 | evidence, it will be sensible to analyse the inherent differences in sensitivity to drought in
440 | cowpea by direct assessment of growth and yield components in the field under typical
441 | production conditions. Slabbert *et al.* [114] noted that whenever the physiological approach is
442 | used in selecting varieties, their performance should be validated in the field under naturally
443 | occurring drought. Agbicodo *et al.* [84] based on a review of several studies identified the
444 | following traits as the more reliable in developing cowpea cultivars with tolerance to drought.
445 | These include determination of chlorophyll fluorescence, stomatal conductance measurements,
446 | abscisic acid measurements, measuring free proline levels, wooden box screening for drought
447 | tolerance at the seedling stage, and delayed leaf senescence.

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

453 | **Effects of water stress on grain nutrient content and phytochemical variability in**
454 | **cowpea seeds under contrasting moisture conditions**

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455 | Pulses are a vital source of plant-based proteins and amino acids for people around the globe and
456 | may be eaten as part of a healthy diet to address obesity, as well as to prevent and help manage
457 | chronic diseases such as diabetes, coronary conditions and cancer; they are also an important
458 | source of plant-based protein for animals [116, 5]. In a study of the phenolic content and
459 | antioxidant properties of selected cowpea varieties tested in bovine peripheral blood. Adjei-
460 | Fremah *et.al.* (2015) reported that, the potential of cowpea polyphenols to reduce oxidative stress
461 | in livestock production is high which is a positive indication for human health improvement.
462 | Viets [118] and Alam [119] reported that, drought reduces both nutrient uptake by the roots and
463 | transport from the roots to the shoots, because of restricted transpiration rates and impaired
464 | active transport and membrane permeability, the decline in soil moisture also results in a
465 | decrease in the diffusion rate of nutrients in the soil to the absorbing root surface [120, 121]. This
466 | will consequently affect the seed yield and the nutritive value of the seed. A study conducted in
467 | Pakistan by [5] on the antioxidant activity of the extracts of some cowpea cultivars commonly
468 | consumed in Pakistan, revealed that, phenolic constituents contained in cowpea may have a
469 | future role as ingredients in the development of functional foods to determine the antioxidant
470 | benefits of the cowpea consumed. The assessment of antioxidant potential might be a fruitful
471 | approach for advocating them as nutraceuticals, in addition to them being potential protein and
472 | carbohydrate sources. The consumption of a processed cowpea would not only improve nutrient
473 | utilization, but also provide potential nutraceuticals for human health. It could therefore be
474 | concluded that cowpea could contribute significantly in the management and/or prevention of
475 | degenerative diseases associated with free radical damage, in addition to their traditional role of

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476 preventing protein malnutrition. Therefore, it will be of immense value to determine the
477 antioxidant, phenolic and other nutritional values of cowpea under contrasting moisture regimes
478 for developed cowpea inbred lines in this study.

479 **Genotype by environment (G x E) interaction**

480 Genotype by environment interaction (G x E) can be defined as the differential response of
481 varying genotypes under change(s) in the environment [122]. The ability, or inability, of
482 organisms to adapt to changes in their environment at the speed necessary, determines the
483 continuation, extinction, or evolution of species [123]. Genotype by environmental interaction is
484 an important factor affecting the breeding and stability of improved and elite genotypes
485 developed through plant improvement programmes in both the developed and developing
486 countries [124] including Ghana. A plant cannot migrate when challenged by fluctuations in
487 environmental conditions, which means that it has to cope with environmental heterogeneity by
488 adapting to the new or fluctuating environment [125]. It can do so via changing the phenotypic
489 expression, a phenomenon called 'phenotypic plasticity', which is often involves altering gene
490 expression and plant physiology in response to environmental signals [126–128]. Scheiner [129],
491 reported that it is not only phenotypic plasticity trait and developmental stage specific but it also
492 often depends on the genotype. When phenotypic plasticity differs between genotypes, this is
493 described as genotype by environment interaction. Dean [130], reported that environmental
494 factors such as temperature, light intensity, and humidity, are the major cause of genotypic and
495 phenotypic variation. Lande and Shannon [131] reported that genotype by environment
496 interaction has heavy implications on the evolution of species, they further on suggest that in
497 constant or unpredictable environments, genetic variance reduces population mean fitness and
498 increases the risk of extinction. Although the importance of the differential effect of the

499 environment on different plant genotypes has been known for a long time and has been
500 considered in crop-breeding programs, it is generally viewed as a thought-provoking issue. When
501 phenotypic plasticity differs between genotypes, this is described as Genotype by environment
502 | interaction. Gerrano *et al.* [132],—_defined an “ideal” test environment, which is a virtual
503 environment that has the longest vector of all test environments (most discriminating) and is
504 located on the AEC abscissa (most representative). Yan *et al.* [133] reported that G and GE must
505 be considered simultaneously in mega-environment analysis, genotype evaluation, and test-
506 environment evaluation; separation of G from GE is primarily a mathematical manipulation that
507 is not always supported by biological evidence combining G and GE in GGE biplot analysis is
508 essential for addressing plant breeding and agricultural problems. The performance of a genotype
509 is determined by three factors: genotypic main effect (G), environmental main effect (E) and
510 | their interaction [134]. Lin and Binns [135]—_introduced a new stability concept as yearly
511 variance within test locations (YV) which relates to stability in time (across years). Also, Lin and
512 Binns [136] defined the superiority index (PI) as the genotype general superiority and defined it
513 as the distance mean square between the genotype’s response and the maximum response over
514 environments. Multilocational trials are necessary in order to confirm the distinctiveness,
515 uniformity and stability of newly developed crop varieties in readiness for recommendation to
516 farmers [137]. Understanding of the genetic variability of cowpea is important to design and
517 accelerate conventional breeding programmes [132]. Collection, characterization and evaluation
518 of available cowpea germplasm, quantification of the magnitude of diversity and classification
519 into groups facilitate identification of genetic variability that enables breeders to select traits of
520 interest for an improvement programme [138, 139]. Therefore, variety trials in a breeding
521 program are usually conducted in several environments, to minimize the risk of discarding

522 genotypes that potentially perform well in some, but not in all, environments; that is, when there
523 is significant G x E and, in particular, when cross-over interaction occurs [140].

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

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

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

534 Farmers' low adoption of technologies developed by research institutions show the need for
535 client-orientation in research and development. The key factors that constrain farmers' adoption
536 of technologies are inappropriateness of the technologies, unavailability of required inputs, and
537 farmers' socio-economic conditions [144]. Therefore, technologies that do not meet farmers'
538 preferences, objectives, and conditions are less likely to be adopted [145].—Farmers are more

539 likely to assess a technology with criteria and objectives that are different from criteria used by
540 scientists. However, farmers' and scientists' criteria for technology assessment must be
541 complementary for effective research and technology development. Farmer evaluations help
542 scientists to design, test, and recommend new technologies to reflect information about farmers'
543 criteria for usefulness of the innovation [146]. In this context, participation is crucial.

544 Participatory research allows incorporation of farmers' indigenous technical knowledge,

545 identification of farmers' criteria and priorities, and definition of research agenda. Participatory
546 Rural Appraisal (PRA) tools were applied to capture farmers' perceptions and fit preferences. De
547 Groote and Bellon [147] and [148], emphasize that participatory approach as Participatory
548 Rural Appraisal (PRA), which involves local people in gathering and analysing information,
549 which allows seeking of insights about local people and their actual conditions, and fosters
550 dialogue between scientists and farmers. By integrating farmers' concerns and conditions into
551 agricultural research, it is hoped that research would develop technologies that become widely
552 adopted, resulting in more productive, stable, equitable, and sustainable agricultural systems.

553 **Markers in cowpea Breeding**

554 Modern technologies, such as marker-assisted selection (MAS), in combination with
555 conventional breeding have been successfully used for genetic enhancement of other crop
556 species. The development and use of biochemical-based analytical techniques and molecular
557 marker technologies, such as restriction fragment length polymorphisms (RFLPs), random
558 amplified polymorphic DNAs (RAPDs), amplified fragment length polymorphisms (AFLPs),
559 and microsatellites or simple sequence repeats (SSRs), have greatly facilitated the analysis of the
560 structure of plant genomes and their evolution, including relationships among the Legumiosae
561 [1, 133, 133, 149]. This in turn has contributed significantly to our current understanding of the
562 cowpea genome organization and evolution. There is a clear need for leveraging modern
563 biotechnological tools to complement conventional breeding in cowpea. Such efforts should
564 focus on the development of molecular markers and protocols for use in marker-assisted
565 selection (MAS) and marker-assisted breeding. [149]. Recently, a Dehydration-Responsive
566 Element-Binding protein2A (DREB2A) ortholog was isolated from cowpea, VuDREB2A
567 (GenBank: JN629045.3) which was highly induced in response to desiccation, heat and salinity,

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568 and conferred enhanced drought tolerance by up regulation of several stress-responsive genes in
569 transgenic *Arabidopsis* [78]. A Ser/Thr-rich region immediately downstream to the DNA binding
570 domain in VuDREB2A appeared to have some role in the stability of the protein, since its
571 removal led to a dwarf phenotype and enhanced expression of some of the downstream genes of
572 VuDREB2A, similar to DREB2A CA [150]. This provides vital clue to the possibilities of
573 existence of similar pathways regulating VuDREB2A in cowpea. A thorough understanding of
574 the molecular mechanisms underlying the stress responses of crop plants, especially tolerant
575 species such as cowpea is necessary for development of enhanced stress-tolerant varieties for
576 sustainable agriculture in the future

577

578 **Conclusion**

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

582

583

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