

## The potential of the African eggplant in production systems under threat from environmental stresses

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### Abstract

Drought, salinity, and increased temperatures are a threat to food security and farmers' income, especially in Africa where around 50% of the population is involved in agriculture. These stresses, often present together in field conditions, damage crops and can reduce yields to a highly detrimental level. To tackle this issue and ensure the availability and affordability of nutritious fresh food, tolerant varieties need to be introduced in production systems. Indigenous vegetables, often overlooked and rarely researched, offer great genetic diversity and tolerance to various stress. The African eggplant, *Solanum aethiopicum*, is indigenous to Africa, highly nutritious, and is present in a wide range of forms, highlighting a great genetic pool. It has the potential to enhance the resilience of agricultural land and ensure food security but is under-researched. This review aims at understanding the state-of-the-art research on *S. aethiopicum* and the effects of abiotic stress on related crops. The first part introduces the African eggplant taxonomy, cultivation, and distribution to understand the current state of this crop in Africa. Then, the effects of drought, salinity, and heat on the *Solanum* genus are reviewed to understand the focus of the current research and up-to-date information on *S. aethiopicum* studies. The effects of biostimulants under stress are also briefly discussed to conclude this review.

*Keywords: Solanum aethiopicum, drought, salinity, heat, indigenous vegetables, food security*

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# 1 Introduction

Sustainable, resilient and reliable food systems are necessary to develop a strong economy and maintain a healthy population. Vegetables and fruits, particularly, are highly nutritious crops containing health-promoting compounds, low in fat, and highly diverse. Vegetable production is, however, facing new challenges around the world due to climate variability [1]. The global average temperature warmed by 0.85°C between 1880 and 2012 and many regions in Africa have experienced greater region-scale warming above 1°C [2]. Extreme conditions, such as heatwaves, drought, or varied rainfall patterns, have also an increased likelihood of happening while high-salinity areas are likely to expand in coastal areas [1]. These changes are expected to reduce crop productivity and modify the nutrition profile of produced food [3].

Abiotic stresses such as drought, heat, and salinity impact negatively every growth stage of many crops by limiting leaf production, reducing photosynthesis and impacting yield [4]. When stress is detected, crops activate a range of responses to survive, which depend on the stress intensity, length, or cultivar studied for example [4]. Despite some common responses to stress, such as the production of reactive oxygen species and associated antioxidative response to limit cell damages, crops also display unique traits depending on their tolerance ability [5]. In addition, the combination of stresses is often observed in natural conditions and has been suggested to lead to new responses by plants, not observed during individual stress, adding to the complexity of predicting how current plants will cope in future production systems [6]. For short-term solutions against the damaging effects of abiotic stress, the use of biostimulants and other growth-promoting compounds has often been investigated and shown some positive results under environmental stress, especially when used in combination [7].

In Africa, agriculture employed more than 50% of the total population in 2017, most of them smallholders who are at the highest risk of threatened livelihood due to climate change [8]. Innovative ways to ensure sustainable and resilient farming are thus needed to ensure food security and reduce poverty. Indigenous vegetables (IVs) are widespread in Africa, are a source of biodiversity, and adapted to local conditions, often displaying tolerance to environmental stresses [9]. Many IVs are nutrient-rich and part of local markets, hence could support and strengthen current agricultural systems to deliver sustainable diets both in terms of human nutrition and environmental issues [10]. The use of IVs to increase field resilience through crop diversity has been limited to date due to the lack of interest and investment [11]. They are under-researched and not used to their full potential, thus not as competitive as main crops such as maize, wheat, or tomato [11]. They include vegetables, such as African eggplant, *Solanum aethiopicum*, Ethiopian mustard, *Brassica carinata*, and okra, *Abelmoschus esculentus*, and legumes including cowpea, *Vigna unguiculata*, and Bambara groundnut, *Vigna subterranea* [9, 12]. *Solanum aethiopicum*, often referred to as African or scarlet eggplant, has received increasing scientific attention due to its high nutritional value, taxon diversity, and market presence in a number of countries [13]. Its stress response pathways have not often been explored, especially under stress combination, limiting its promotion and use to farmers and seed producers.

Crucial information is thus still missing to understand the impact of climate change and develop adaptation strategies for resilient systems [14]. This review highlights the latest research on *Solanum aethiopicum*, reviews the effects of drought, heat and salinity on *Solanum* crops, in particular *Solanum aethiopicum*, and investigates some methods used to improve stress tolerance.

## 2 *Solanum aethiopicum*

### 2.1 Taxonomy and genetics

The African eggplant (*Solanum aethiopicum*) originates from Africa and has been domesticated from *S. anguivi*, still found in the wild [15]. *S. aethiopicum* is a close relative to the common

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48 Brinjal eggplant from Asia (*S. melongena*) and tomato (*S. lycopersicum*) and is also a relative of  
49 other indigenous *Solanum* such as the Gboma eggplant (*S. macrocarpon*) [16]. *S. aethiopicum* is a  
50 complex hermaphrodite species consisting of four groups distinct both morphologically and in their  
51 use: shum, gilo, kumba, and aculeatum [17, 18]. Figure 1 shows fruits on plants of gilo, kumba,  
52 and shum cultivars.

53 Only the small, hairless leaves from shum plants are commonly eaten, while their highly bitter  
54 small fruits growing in clusters are used to collect seeds [19]. Shum varieties are found in the higher  
55 rainfall zones of West and Central African countries, or grown in swamps during the dry season  
56 [20]. Due to the recurrent shoot and leaves harvest for selling, plants are not able to grow and will  
57 develop instead a much-branched architecture with weak stems and many small laves, preferred by  
58 the consumers [20].

59 The gilo group is highly common in humid areas and plants from this group display inedible  
60 hairy leaves and edible green or white fruits, which can be round, elongated, ribbed or smooth [19].  
61 They usually have 1-3 fruits per node and the bushy plants can reach up to 2 m, even though most  
62 commercial varieties range from 65 to 110 cm in height [20]. Gilo plants grow well at a temperature  
63 between 25 and 35°C during the day and 20-27°C at night [21]. Due to Gilo's higher morphological  
64 complexity than Shum, it has been suggested that the former have evolved from the latter.

65 Plants from the kumba group, most commonly found in arid areas, have hairless leaves and  
66 medium to big ribbed fruits, both edible [19]. Plants from this group do not grow very tall, around  
67 40-50 cm [20]. Nowadays, Kumba varieties with hairy leaves and only grown for their fruits are  
68 preferred in some regions due to their increased tolerance to pests [20]. Kumba plants tolerate high  
69 temperatures, up to 45°C during the day [21].

70 Finally, plants from the aculeatum group produce inedible fruits and leaves, mostly used as  
71 ornamentals, and are the least common group grown in Africa [19].

72 Each group is hypervariable with hundreds of local varieties across Africa [22]. Within each  
73 group, sub-groups can be distinguished based on various metrics such as fruit shape or size. Traits  
74 have evolved through time based on farmers' and consumers' selection, leading to very diverse fruits  
75 across the continent. Phenotypic variations can be observed at all developmental stages, offering  
76 great breeding potential due to the high genetic pool still present within the *S. aethiopicum* species  
77 [23].

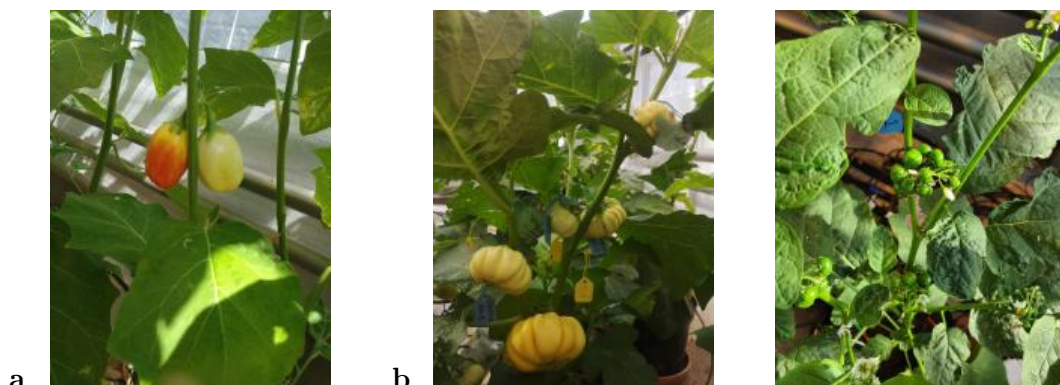


Figure 1: African eggplant (a) Gilo, cv. DB3 (b) Kumba, cv. Mekevan (c) Shum, cv. E11 grown at NIAB East Malling, UK.

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## 78 2.2 Cultivation

79 Seeds of fruity varieties of the African eggplant are sold by various seed producers such as Similaw  
80 Seeds, Lagrotech Seeds, and Rijk Zwaan. Farmers, however, will generally collect their seeds by  
81 leaving the berries to dry out and extract them when ready to plant or by extracting the seeds at  
82 harvest directly from ripe fruits and drying them for long-term storage [19].

83 The African eggplant is mostly grown by small-scale farmers, accounting for 80% of the total  
84 production, mostly women [24]. It is a perennial crop but the yield is dramatically reduced after the  
85 first season [20]. Most commercial plants will thus be kept alive for one season of about six months  
86 before being removed to make space for new seedlings that will be planted for the following rainy  
87 season. As this crop is mostly rain-fed, it is primarily cultivated during the rainy season but can  
88 be grown during the dry season in the case farmers have access to irrigation [25]. Even though the  
89 total production will be lower than in the wet season, the market price of fruits produced during  
90 the dry season will be at its highest, increasing the farmers' income drastically [24]. To promote  
91 growth and income stability, the African eggplant is often intercropped with profitable crops such  
92 as *Amaranthus lividus* in Uganda [26].

93 Nitrogen, selenium and potassium are the most limiting nutrient in African eggplant growth  
94 [27]. Fertiliser input is, however, not a common practice in small-scale cropping systems due, in  
95 part, to the lack of availability and high price. Instead, manure is commonly used by farmers to  
96 enhance crop vitality [25].

97 Leaf harvest from Shum varieties usually starts two months after sowing and can be repeated  
98 up to five times through one season [20]. Flowering, pollination and fruit formation for fruity  
99 varieties generally start a month and a half after transplanting in the field while fruits are typically  
100 ready to harvest about one month after fruit set [21]. The earliest varieties belong to the kumba  
101 group and can be harvested at about 85 days from sowing while most varieties require 110-120 days  
102 [20]. During the harvest season, fruits can be harvested twice a week to avoid quick over-ripening  
103 and promote plant vigour but are most generally harvested every 5 to 6 days to balance harvested  
104 quantity with cost [28].

105 Fruit weight ranges from 25 to 110 g and yield varies significantly between areas, from 0.1 t/ha  
106 to 7.7 t/ha, and reaching sometimes 20 t/ha under irrigation [12, 21]. In Ghana, for example, the  
107 yield peaked at 7.89 t/ha in 1997 but is now decreasing with a report of only 1.97 t/ha in 2004  
108 [28]. Improved cultivars under favourable conditions have shown drastic yield improvement reaching  
109 around 60 t/ha [29]. Leaf yield averages at 30 t/ha despite a potential of 225 t/ha under specific  
110 farming management [21].

111 In addition to being cultivated for its fruits or leaves, *S. aethiopicum* has also attracted attention  
112 as a potential rootstock for close relatives such as the tomato or brinjal eggplant to enhance  
113 plant vigour and/or tolerance against certain soil-born pathogens [30]. Indeed, as interspecies  
114 hybridisation can sometimes face challenges such as infertility or incompatibility, the reliance on  
115 rootstock in commercial farms is more common to provide resistance against important soil-born  
116 pathogens [31].

## 117 2.3 Distribution and use

118 *S. aethiopicum* is popular in sub-Saharan countries such as Tanzania, Uganda, Benin, Mali, or  
119 Ghana, and is also being grown in Brazil under the name 'jilo' [12, 17]. The fruit is consumed in  
120 East Africa while leaves are primarily consumed in Uganda and both leaves and fruits are eaten in  
121 West Africa [12]. Marketable fruits are creamy to green in colour, while red and ripe fruits are used  
122 to collect seeds but not eaten [12]. In cuisine, it is used similarly to tomato in stews to accompany  
123 local dishes or as soup thickeners, but the fruit can also be eaten raw [28]. The highly bitter fruits  
124 of some cultivars, as well as the roots, are sometimes used as medicine to treat colic, and high blood  
125 pressure or to treat uterine complaints [21]. Size, colour, taste and shape are the main attributes  
126 checked by consumers, with a preference for non-rounded shaped fruits due to their association with

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127 a reduced bitterness [28]. Consumers are particularly attracted to the medicinal value and good  
128 nutritional value of the fruits and leaves.

129 The low shelf-life of the African eggplant fruits, from 3 to 7 days, leads to significant postharvest  
130 losses and drying the product has been suggested to counteract the waste produced [17]. Despite  
131 increasing shelf-life, drying methods reduce the pharmaceutical activity of the product and can be  
132 expensive, thus are still only sparsely used [32].

133 The African eggplant price fluctuates highly during the year, reaching a peak during the dry  
134 season and a low in the rainy season [28]. The lack of product uniformity, quality standards, general  
135 price information, and unstable supply lead to large price fluctuations between regions which, in  
136 turn, limits farmers' investment in the African eggplant as their main cultivated crop [28].

## 137 2.4 Nutritional and pharmaceutical properties

138 *S. aethiopicum* fruits have a high moisture content and very low caloric value and provide several  
139 fundamental mineral elements such as calcium, iron, zinc and vitamins [33]. Fruits and leaves  
140 contain many phytochemicals, such as phenols, saponins, and flavonoids, which can benefit human  
141 health but are also important as secondary metabolites to protect the plant from stress [17]. Kumba  
142 plants tend to have the highest level of antioxidant activity while aculeatum plants seem to have the  
143 lowest nutritional value, highlighting a potential selection by growers and consumers for nutritious  
144 varieties. Different cultivars, even within the same group, can display high variability in nutritional  
145 quality as shown by Nwanna, Adebayo, Ademosun, and Oboh [34] when assessing fruits from two  
146 markets and recording large differences in total phenols (253 vs 499 mg gallic acid equivalent/100g),  
147 total flavonoids (154 vs 392 mg quercetin/100g), and total antioxidants (1.24 vs 3.50 mmol trolox  
148 equivalent antioxidant capacity/g).

149 *S. aethiopicum* is used in traditional medicine to treat different conditions such as mental  
150 disorders or diabetes [21, 35]. Due to the high antioxidant levels within the plant, they have been  
151 suggested to be used as nutraceutical supplements [36]. The supplementation of diets with dry or  
152 fresh leaves from the African eggplant has been investigated in multiple studies which have seen  
153 some beneficial effects on obesity development [37], ulcers formation [38] or iron intake [39] for  
154 example. Red fruits displayed higher levels of essential minerals, highlighting a potential to dry  
155 these fruits instead of marketable ones to obtain a highly nutritional powder while limiting waste  
156 and increasing farmers' income [40].

## 157 2.5 Breeding and genetic resources

158 The African eggplant is considered an 'orphan crop' due to the low scientific and institutional  
159 support received in the past. It is now gradually being taken up in breeding programs due to its  
160 high genetic diversity, good nutritional quality, and high tolerance to certain biotic and abiotic  
161 stress [41].

162 A major part of the currently grown varieties is a result of farmers' selection based on their  
163 or the consumers' preferences. Nevertheless, 98% of the commercial seeds in East and Southern  
164 Africa in 2014 were improved varieties developed by the World Vegetable Centre (WVC) [42]. This  
165 number does not translate to the most commonly grown varieties yet as most farmers will use  
166 their own seeds rather than the commercial ones, as stated above. WVC has been working on  
167 African eggplant varieties since 1993 and released multiple cultivars, such as the highly popular gilo  
168 cultivar in Tanzania in 2006 called DB3 [43]. In 2016, the WVC selected the African eggplant as  
169 a major strategic crop for breeding based on its importance in African countries, nutritional value  
170 and income generation potential [12]. There is a high genetic diversity for the African eggplant  
171 with 798 genebank accessions conserved worldwide, 481 by the WVC [18]. Farmers across Africa  
172 keep a large genetic resource as each region seems to have a preference for different morphological  
173 traits and is thus cultivating their own local varieties of African eggplant [17]. As the same variety

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174 cultivated in different regions can have a different name, recording the actual diversity is sometimes  
175 a challenge [28].

176 Some breeding programs for the African eggplant started already in the last 80s. Nowadays,  
177 a few companies have active breeding programs and are selling improved cultivars such as Rijk  
178 Zwaan and East-West Seeds in Tanzania, or Technisem in Senegal. Their distribution systems are  
179 limited to a few countries, however [17]. Despite the vast genetic material available for African  
180 eggplant breeding, the lack of characterisation and trait evaluation has limited progress so far. The  
181 recently published draft genome sequence of the African eggplant shed light on genes associated  
182 with disease resistance and drought tolerance [44]. It is an important step to speed up cultivar  
183 development through targeted genetic modifications and for the development of molecular markers  
184 that could be used as a diagnostic tool at the seedling stage in breeding [45].

185 Since gene transfer between eggplant species is possible, *S. aethiopicum* is acknowledged as a  
186 source of variations in brinjal eggplant breeding as well [46]. This was shown early on by multiple  
187 studies which successfully introduced resistance to bacterial wilt [47] or *Fusarium* wilt resistance  
188 in *S. melongena* [48], a soil-borne disease for which *S. aethiopicum* is resistant. In addition to  
189 breeding for pathogens tolerance, looking into genes associated with abiotic stress tolerance and  
190 resistance such as drought has also been investigated. Sseremba, Tongoona, Eleblu, Danquah, and  
191 Kizito [49] conducted a study on shum hybrids under different watering conditions to determine the  
192 heritability of drought resistance for breeding programs. Leaf relative water content, plant height  
193 and the number of leaves per plant were determined to be of high importance, in this order, for  
194 breeding a stable increased performance under drought stress.

### 195 3 Abiotic stress in *Solanum*

196 Abiotic stresses trigger some responses shared between plants, such as the triggering of osmotic  
197 stress, but also lead to individual responses based on species, intensity, length and developmental  
198 stage [4]. The effects of drought, heat, salinity and their combination on *Solanum* crops, with a  
199 focus on *Solanum aethiopicum*, are explored below.

#### 200 3.1 Drought

201 Drought stress is one of the most damaging factors in crop production with effects on plants'  
202 morphology, physiology, and biochemical processes [50]. Table 1 depicts graphically some of the  
203 literature available on drought effects on *Solanum* species.

##### 204 3.1.1 *Solanum aethiopicum* under drought

205 In a study by Lagat [51], a range of morphological and physiological aspects of *S. aethiopicum* were  
206 decreased in every accession tested under reduced field capacity at a different rate for each accession.  
207 For example, under a 20% irrigation reduction, stomatal conductance decrease ranged from -6% to  
208 -40% with an average of 19% [51]. The variability observed highlights the range of tolerance among  
209 cultivars despite the absence of absolute tolerance of morphological and physiological metrics. In  
210 addition, fruits' sugars, acids, beta-carotene, and vitamin C increased under 60% field capacity,  
211 highlighting the activity of the plant's secondary metabolism [51]. These benefits were, however,  
212 counter-balanced by a decrease in mineral elements such as magnesium, calcium, iron and zinc,  
213 reducing the overall increase in fruits' nutritional quality [51].

214 Another study investigating drought effects on the African eggplant secondary metabolism also  
215 showed high variability between accessions [52]. Out of the 19 accessions tested, 10 displayed an  
216 increase in total carotenoids, 5 a decrease and 4 no change [52]. Each carotenoid was affected  
217 differently as well, with an overall decrease in chlorophylls and carotenes and an increase in  
218 xanthophyll, suggesting a decrease in leaf pigmentation alongside an increase in other dietary

Table 1: Sub-sample of the available studies on the effect of drought on *Solanum* species.

Species						Responses										Reference			
<i>S. aethiopicum</i>	<i>S. lycopersicum</i>	<i>S. melongena</i>	<i>S. insanum</i>	<i>S. incanum</i>	<i>S. anguivi</i>	% Pot / field capacity	Shoot biomass	Leaf area	Plant height	Yield	Membrane stability	Stomatal conductance	Photosynthesis activity	Chlorophyll	Sugars		Non-enzymatic antioxidants	Enzymatic antioxidants	
						40		↓	↓	↓		↓		↓			↑		[51]
						45						↓	↓	↓	↓	↓		↑	[70]
						40				↓				↓	↑				[78]
						25	↓			↓									[56]
						50	↓	↓	↓					↓		↑	↑		[59]
						Wilting	↓								↓	↑	↑		[77]
						50				↓		↓	↓	↓					[55]
						50			↓			↓	↓	↓					[61]
						No water	↓									↓	↓		[63]
						No water	↓									↑	↓		[63]

219 neutraceutical carotenoids [52]. Further to their carotenoids study, Mibei, Owino, Ambuko,  
 220 Giovannoni, and Onyango [53] analysed a range of metabolites in the leaf extract, including organic  
 221 acids, sugars, and amino acids. Similarly, accessions reacted differently even though a general trend  
 222 of increasing sugars and organic acids appeared [53]. The authors shed light on important parts  
 223 of the oxidative responses to drought in various African eggplant accessions and highlighted key  
 224 metabolites involved in drought stress adaptation. The high diversity between accessions observed  
 225 shows the great potential for nutritious and tolerant species to be selected for farming.

226 When using one variety in the field, Mwinuka, Mbilinyi, Mbungu, Mourice, Mahoo, and  
 227 Schmitter [27] demonstrated that watering at 80% of the crop requirement was optimal to balance  
 228 the cost of irrigation while maintaining the same yield. Similarly, gilo cultivar Morro Grande had  
 229 a reduced plant growth and fruit yield only at 50% irrigation reduction but not at 25%, showing  
 230 a good tolerance threshold [54]. In another study, a drop from 100% pot capacity to 75% reduced  
 231 a variety of morphological attributes such as leaf number, area and plant height, even though a  
 232 reduction to 50% did not damage these characteristics further [55]. Photosynthesis and fruit yield,  
 233 in opposite, were maintained at 75% pot capacity [55]. The African eggplant pathways to tolerance  
 234 are thus varied and the conservation of fruit production over vegetative growth seems to be in  
 235 place under low-intensity drought. Different responses were also noted when drought was applied  
 236 at different growth stages with the flowering stage being the most critical stage for watering [56].  
 237 This knowledge is important for farmers to ensure crop protection at key growing points.

238 The responses of *S. aethiopicum* genetic populations or individual cultivars under deficit  
 239 irrigation shed light on exciting varieties to use in dry conditions and paved the way for breeding.  
 240 Further studies need to encompass the wide range of existing cultivars and understand the different  
 241 tolerance mechanisms and stress thresholds of *S. aethiopicum* due to the variability of results  
 242 observed.

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### 243 3.1.2 *Solanum* species under drought

244 Morphological defects caused by drought can already be noticed at the seedlings stage with a reduced  
245 germination rate and seedling growth in eggplant under water stress [57]. Later on, eggplant leaf  
246 development was reported to be slowed by drought by Kirnak, Kaya, Tas, and Higgs [58], an  
247 adaptation mechanism used to limit water loss. A reduction of leaf area was also noted in tomato  
248 by Kusvuran and Dasgan [59] with the maintenance of leaves number, supporting the production of  
249 smaller leaves instead. This observation was also made by Zhou et al. [60] in two different tomato  
250 cultivars. Even if drought impacts morphological characteristics at every growth stage, a study  
251 by Ghannem, Ben Aissa, and Majdoub [61] showed that yield and fruit characteristics of tomato  
252 were only impacted when drought was applied at the harvesting stage, suggesting the presence of  
253 recovery mechanisms earlier. Fruit characteristics were also impacted in eggplant under drought  
254 with a reduction in diameter and length, reducing eventually marketable yield and the profitability  
255 of this crop [62].

256 Root length was reduced for multiple tolerant and susceptible eggplant cultivars under no  
257 irrigation [63]. Root dry weight, however, was not reduced for tolerant eggplant cultivars in another  
258 study, showing diverse responses of root development by producing either more small roots or larger  
259 roots [63]. While drought avoidance mechanisms can lead to an extended root network to access  
260 water more easily, especially in the field, the reduction in root growth is often seen as a tolerance  
261 mechanism in order to maintain resources. Stem development is also hindered by the lack of water  
262 with plants producing stems of smaller diameters and reducing shoot dry weight overall, as observed  
263 in eggplant [58] and tomato [64]. These reductions seem to only appear after a certain threshold  
264 with a reduction in irrigation by 20% or 25% not impacting significantly eggplant development  
265 and yield, as seen before [65, 66]. Under higher intensity, however, the reduction of stem diameter  
266 eventually leads to reduced water and nutrient flow within the plant.

267 Reducing water flow through the plant affects plant water status whose maintenance is crucial  
268 for many physiological processes [67]. A decrease in leaf relative water content (LRWC) has regularly  
269 been reported under drought in eggplant [58] and tomato [68] and is now a common stress marker. A  
270 decrease has even been noted in a drought-tolerant tomato cultivar, even though a sharper decrease  
271 was observed in a sensitive cultivar [59]. This decrease is generally observed even at a low level of  
272 drought and at early stages, highlighting the quick response of this marker [67]. A quick recovery is  
273 also noted after re-wetting soil as observed in eggplant [69]. The reduction of LRWC enables plants  
274 to withstand drought periods better by reducing water loss through leaves but limits cell expansion  
275 and other processes.

276 A decrease in water status is a signal for plants to close their stomata in order to limit further  
277 water loss through transpiration [50]. This closure was noted in tomato even at a low-stress level  
278 of 15% irrigation reduction and at every growth stage [60, 61, 68, 70]. Stomatal closure has been  
279 generally said to be the main driver for decreased photosynthesis under drought, eventually leading  
280 to reduced fruit production. Other mechanisms can, however, decrease photosynthesis following  
281 drought as well due to the complex photosynthetic mechanisms. For example, drought often leads  
282 to a reduction in chlorophyll production as reported in *S. melongena* [71] and *S. lycopersicum* [72],  
283 eventually reducing the light-harvesting capacity of the plants. In a study by Çelik, Ayan, and Atak  
284 [68] in tomato, leaf photosynthetic pigments were reduced two days after the beginning of stress,  
285 showing a dynamic and fast process. A chlorophyll decrease in tomato was most prevalent during  
286 the vegetative stage, when sufficient photosynthesis activity is crucial to develop resources to start  
287 flowering, and at fruit set [61]. Nonetheless, chlorophyll can also increase in some cultivars under  
288 water stress as seen in eggplants by the study of Mahammed, Babu, Lakshmana, Ganapathi M,  
289 and Rakshith [73]. This increase, measured per leaf area, can be due to the smaller leaves observed  
290 under drought, leading to a higher concentration of chlorophyll per area but can also be an intrinsic  
291 mechanism to enhance light harvest while limiting water loss. Alongside photosynthesis pigments,  
292 membrane stability is crucial to maintain photosynthesis activity [50]. Under drought, membrane  
293 stability, measured by the amount of electrolyte leakage, has regularly been reported to increase

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294 proportionally to the level of stress in eggplant and tomato [73, 74]. Leakage of electrolytes has  
295 often been related to photosynthetic and mitochondrial activity reductions in plants.

296 Net photosynthesis rate has been observed to decrease sharply under the absence of irrigation  
297 in tomato [60]. Limited irrigation also increased non-photochemical quenching in the same study,  
298 showing an adaptive process to limit the creation of reactive oxygen species (ROS) produced due to  
299 the imbalance of the energy harvested and its utilisation [75]. ROS, while beneficial for plant stress  
300 response at low levels as signalling molecules, can have damaging effects on cells when present at a  
301 high concentration and lead to oxidative stress [76]. Malondialdehyde (MDA), a marker of oxidative  
302 stress, increased gradually as pot water content decreased in tomato, as did total protein content  
303 driven by a sharp increase in antioxidant enzymes [68]. Interestingly, levels of MDA were similar  
304 between tolerant and susceptible eggplant cultivars in a study by Plazas et al. [63], highlighting  
305 that MDA levels do not automatically translate to plant tolerance.

306 In a study on one tomato cultivar, drought stress increased oxidative stress alongside enzymatic  
307 and non-enzymatic antioxidant levels as a response [72]. Lycopene, a major antioxidant in tomato,  
308 increased under stress in three cultivars with phenols, flavonoids, and total antioxidants [77].  
309 Antioxidants are the main defenders to limit ROS damage and maintain cell processes [76]. When  
310 comparing susceptible, intermediate, and tolerant eggplant cultivars, Plazas et al. [63] showed that  
311 even if all accessions had an increase in phenols and flavonoids, this increase was more important  
312 for tolerant cultivars. The same observation was made for the antioxidant enzyme catalase, while  
313 only susceptible and intermediate cultivars increased their levels of ascorbate peroxidase, another  
314 antioxidant enzyme [63]. The antioxidative response is thus tightly controlled under stress with  
315 selected enzymes and non-enzymatic antioxidants being activated under certain conditions. Some  
316 cultivars seem to rely on their antioxidant activity for stress tolerance, ensuring cell processes are  
317 maintained and damage by ROS compounds is limited.

318 Other biochemical processes are affected by drought due to the reduction in mineral elements  
319 uptake by the roots and the following reduction in the distribution of these elements to the different  
320 plant organs. Leaf nitrogen, potassium and phosphorus decreased in *S. melongena* grown at 80%  
321 pot capacity in two experiments [58, 71]. A further reduction in irrigation level was needed before  
322 observing a reduction in these minerals in a study by Mohawesh [78], suggesting the involvement  
323 of a genetic factor in the maintenance of the uptake of these elements. This was also observed in  
324 tomato cultivars where most cultivars had a reduction in their leaf nitrogen levels under drought  
325 except the tolerant ones [79]. In the same study, potassium, phosphorus, magnesium and iron were  
326 unchanged in the sensitive cultivars but were increased in the most tolerant cultivar, highlighting  
327 the importance to enhance selected mineral elements to promote tolerance by maintaining plant  
328 growth and photosynthetic activity [79].

## 329 3.2 Heat

330 Elevated temperatures or extreme events such as heatwaves can hinder plant growth at every  
331 development stage depending on cultivar, intensity and length of stress as discussed by multiple  
332 reviews [80–82]. In addition to morphological and physiological changes, antioxidant levels can  
333 also be affected by heat stress and increase a plant's nutritional value [82]. Short, measured stress  
334 can thus be beneficial, if timed right, for vegetable quality by improving human health-promoting  
335 compounds. Table 2 depicts graphically some of the literature available on the effects of high  
336 temperatures on *Solanum* species.

### 337 3.2.1 *Solanum aethiopicum* under heat

338 *S. aethiopicum* L. cv. Legon Prolific, a gilo cultivar, has been shown to have an increased  
339 photosynthesis activity and stomatal conductance between 30°C and 35°C but decreased at 40°  
340 C, showing a high tolerant threshold [83]. Plant height and shoot weight, conversely, increased

Table 2: A sub-sample of the available studies on the effect of heat on *Solanum* species.

Species			Responses											Reference		
<i>S. aethiopicum</i>	<i>S. lycopersicum</i>	<i>S. tuberosum</i>	Heat (°C)	Shoot biomass	Leaf area	Plant height	Yield	Pollen germination	Membrane stability	Stomatal conductance	Photosynthesis activity	Chlorophyll	Sugars		Non-enzymatic antioxidants	Enzymatic antioxidants
			40	↑		↑	↓			↑	↓					[83]
			45					↓		↑	↓					[93]
			36					↓		↓	↓	↓	↑	↓		[91]
			30			↓						↓			↑	[94]
			35				↓				↓	↓			↑	[95]
			36			↓				↑	↓	↓	↑			[84]
			35			↑	↓					↑				[87]
			38	↓	↓			↓		↑	↓					[89]
			45							↓	↓	↓	↑			[90]
			38	↓						↓	↓	↓			↑	[96]

341 under 40°C [83]. Despite an enhancement of vegetative growth under heat, fruit numbers decreased  
 342 drastically and the overall yield was reduced even though the fruits produced were heavier [83].  
 343 Further research on the heat tolerance of *S. aethiopicum* has not been conducted, limiting empirical  
 344 data available to promote its use in heat-prone land.

### 345 3.2.2 *Solanum* species under heat

346 The vegetative growth of tomato plants was unaffected in a study subjecting them to a 10°C increase,  
 347 reaching 36°C, as seen by the absence of changes in plant height, leaf number and stem diameter in  
 348 both heat-tolerant and heat-sensitive cultivars [84]. When including more cultivars and setting the  
 349 temperature at 40°C, Sherzod, Yang, Cho, Chae, and Chae [85] found an increase in plant height  
 350 and stem diameter for many cultivars, especially the ones producing large fruits. Blanchard-Gros,  
 351 Bigot, Martinez, Lutts, Guerriero, and Quinet [86] also found a cultivar-dependent response of plant  
 352 height under heat when studying *S. chilense* with the increase in stem growth under heat for some.  
 353 The same trend regarding plant height was noted in potato, *Solanum tuberosum*, with an increase  
 354 of 13°C from normal temperature leading to a plant height increase of 47% on average [87]. The  
 355 positive effect of heat on plant development seems thus to appear mostly at very high temperatures  
 356 in *Solanum*. Interestingly, when including a recovery period, Duan et al. [88] showed that even  
 357 after no effects on stem growth during the heat period, tomato plants that experienced heat had a  
 358 slower growth development when placed back under normal temperature than the controls. This  
 359 observation supports long-term damages and a slow recovery regarding vegetative growth.

360 Leaf production and development are, in general, hindered at high temperatures as seen in both  
 361 tolerant and sensitive tomato cultivars [89] and potato [90] after a certain threshold. No change in

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362 leaf number was noted, however, in young tomatoes grown at 36°C and leaves produced were the  
363 same size in another study growing tomatoes at 40°C [84, 85]. The different growth stages and stress  
364 lengths, with the latter studies focusing on short-term stress at early stages, might explain these  
365 antagonist effects observed. Under heat stress, smaller leaves are a way to limit excess transpiration  
366 and water loss.

367 Leaf pigments are also affected by heat with tolerant tomato cultivars displaying higher leaf  
368 pigment levels in a study by Zhou, Yu, Kjær, Rosenqvist, Ottosen, and Wu [91]. Every potato  
369 cultivar investigated by Tang et al. [87] also displayed higher leaf pigment levels under heat.  
370 Chlorophyll b tends to increase to a lesser extent than chlorophyll a due, in part, to its high  
371 correlation with light-harvesting proteins [92, 93]. A high number of light-harvesting proteins  
372 can be nefast for plants under stress as the excess light not used in the photosynthesis process  
373 can damage the photosynthesis apparatus and other processes. An increase in chlorophyll a is  
374 nonetheless important to maintain photosynthesis. In addition, an increase in chlorophyll a and  
375 carotenoids can lead to the reduction of photooxidation and photoinhibition by ensuring excess  
376 light is dissipated as heat [75]. As opposed to the previous observation, a potato cultivar tolerant  
377 in regard to micro tuber formation showed a slight decrease in leaf pigment, especially chlorophyll  
378 b, showing that other tolerance mechanisms are in place to ensure fruit production, in this case  
379 [94]. A range of studies supported that observation with a reduction in leaf pigments in potato [95],  
380 tomato [96], or eggplant [97].

381 Tolerant tomato cultivars displayed an increase in stomatal conductance which was not  
382 observed in sensitive ones [91]. Both sensitive and tolerant tomato cultivars increased their  
383 stomatal conductance under heat in another study, however, suggesting a variation in the tolerance  
384 mechanisms [89]. This adaptive mechanism allows better leaf cooling and the maintenance of  
385 enzyme activity, crucial to maintaining photosynthesis. This was not observed by Zhou, Kjaer,  
386 Rosenqvist, Yu, Wu, and Ottosen [84] and Duan et al. [88] who reported a decrease in stomatal  
387 conductance in tomato plants, suggesting different mechanisms in play to limit water loss despite  
388 increasing leaf temperature. The photosynthesis apparatus is, in general, highly disturbed by heat  
389 through a range of mechanisms including enzyme denaturation and increased transpiration [82].  
390 Photosynthetic parameters were reduced in tomato plants subjected to an increase of 15°C or  
391 higher [98, 99] but no negative effects were noted at a 6°C increase in another cultivar [60]. The  
392 photosynthetic rate of *S. lycopersicum* was reduced at both seedling and anthesis stages under heat  
393 but only in the sensitive cultivar Zhou, Kjaer, Rosenqvist, Yu, Wu, and Ottosen [84]. Maximum  
394 photochemical efficiency of photosystem II ( $F_v/F_m$ ) can be a powerful way of identifying heat  
395 tolerant plants as the maintenance of  $F_v/F_m$  under heat stress is associated with multiple other  
396 tolerance traits [89, 91]. As a fast-responding indicator of a plant's photosynthesis efficiency,  $F_v/F_m$   
397 can help researchers quickly identify damage to the photosynthesis process.

398 Despite the boost sometimes observed in the vegetative growth of *Solanum* plants, the most  
399 drastic effects of heat stress are observed during the reproductive stages, hindering final fruit yield  
400 [100]. In tomato, both short and long-lasting heat stress reduced pollen germination and the number  
401 of fruits produced [85, 101]. Pollen germination was decreased in both tolerant and sensitive tomato  
402 cultivars even though the effects were most noticeable in the sensitive one [91]. Pollen tube length,  
403 on the other hand, was not affected by a 10°C increase in tolerant tomato plants but decreased  
404 strongly in sensitive ones [91]. In one study, the number of flowers increased significantly under  
405 heat despite a net reduction in fruit yield, showing that pollen defects are the main reason for a  
406 reduced fruit set and yield [102].

407 Oxidative stress, as measured by hydrogen peroxide ( $H_2O_2$ ) concentration or lipid peroxidation,  
408 was induced by heat in tomato [99, 103]. To counteract this increase, crops, in particular tolerant  
409 cultivars, can enhance their antioxidant metabolism as was seen by an increase in phenols and  
410 antioxidant enzymes [95, 96, 104]. Osmolytes are also often increased to maintain membrane  
411 stability and a range of cell processes, as was observed in a study by Dasgan, Dere, Akhoundnejad,  
412 and Arpacı [104] with an increase in sugars in both tolerant and susceptible tomato cultivars.

413 Proline is also increased by heat in *Solanum* to maintain cell turgor and expansion, an adaptive  
 414 mechanism to tolerate short-term heat stress [90, 99].

### 415 3.3 Salinity

416 Saline soils contain excessive soluble salts, mainly sodium chloride (NaCl) and sodium sulphate  
 417 ( $\text{Na}_2\text{SO}_4$ ), and are generally described as having an electrical conductivity higher than 4 dS/m  
 418 [105]. This represented 412 million hectares of soil in 2015, 122.9 of which in Africa [105]. Different  
 419 salinity intensities are further defined as seen in Table 3. Salinity disturbs every growth stage  
 420 of crops, especially during seedling development, via osmotic or ion-excess responses [106]. The  
 421 former is due to the lower uptake of water by the plant due to the high salt concentration in soil  
 422 and has a rapid onset, while the latter is caused by the excessive uptake of  $\text{Na}^+$  and  $\text{Cl}^-$  over a  
 423 long exposure period. A range of processes is affected by salinity in Solanaceous crops including  
 424 morphological, physiological and molecular pathways [107]. Table 4 depicts graphically some of the  
 425 literature available on salinity effects on *Solanum* species.

Table 3: Soil salinity classes in electrical conductivity  $\text{EC}_e$

Salinity rating	Non-saline	Weakly saline	Moderately saline	Strongly saline	Very strongly saline
$\text{EC}_e$ (dS/m)	< 2	2 - 4	4 - 8	8 - 16	> 16

#### 426 3.3.1 *Solanum* species under salinity

427 Salinity stress affects *Solanum* species from the germination stage, with both *S. lycopersicum* and  
 428 its close relative *S. nigrum* displaying reduced seed germination under NaCl irrigation, even if the  
 429 wild *S. nigrum* was less affected [108]. Of the germinated seeds, both root and shoot growths  
 430 were limited by the stress [108]. This negative effect on root and shoot was also observed in the  
 431 plants' vegetative stages [109, 110]. Interestingly, even high levels of salt did not reduce plant  
 432 growth parameters in *S. insanum*, a wild ancestor of the brinjal eggplant, highlighting the tolerance  
 433 potential of *Solanum* species [110]. Another study showed a reduction in final yield but no signs  
 434 of stem diameter or root length defects on the brinjal eggplant under high salinity levels, showing  
 435 variations between accessions and stress length [111]. In *S. melongena*, root growth was even  
 436 promoted under salinity and stem and leaf development was maintained, even though this was not  
 437 sufficient to maintain final yield [112]. *S. pennelli*, a salt-tolerant crop, formed the central focus  
 438 of a study by Albaladejo, Meco, Plasencia, Flores, Bolarin, and Egea [113] in which the authors  
 439 found a slow tolerance mechanism. When compared to *S. lycopersicum*, shoot and root growth  
 440 rate was much slower in the tolerant crop than in tomato after seven days of stress, but this was  
 441 reversed after 14 days [113]. Due to the two-step toxicity mechanism of salinity, tolerance can take  
 442 place at different stages and might only be perceived when a threshold is passed. Growth stages  
 443 also seem to affect greatly how plants react to salinity stress with an increased tolerance at later  
 444 stages [114]. Leaf development was reduced in *S. melongena* at lower salinity levels than stem or  
 445 root development, showing differences between plant organs [110]. This decrease in leaf production  
 446 was also observed in *S. nigrum* [109], *S. insanum* [115], *S. lycopersicum* [116] and *S. chilense* [117].  
 447 The tolerant *S. pennelli* maintained leaf thickness under salt while the sensitive *S. lycopersicum*

Table 4: Sub-sample of the available studies on the effect of salinity on *Solanum* species.

Species						Responses										Reference			
<i>S. lycopersicum</i>	<i>S. melongena</i>	<i>S. tuberosum</i>	<i>S. insanum</i>	<i>S. nigrum</i>	<i>S. chilense</i>	Growth media	Shoot biomass	Leaf area	Plant height	Yield	Stomatal conductance	Photosynthesis activity	Chlorophyll	Sugars	Leaf sodium (Na)		Leaf potassium (K)	Non-enzymatic antioxidants	Enzymatic antioxidants
						Pot	↓	↓	↓	↓					↓	↓			[111]
						Hydroponics	↓							↑	↓				[130]
						Pot	↓	↓	↓				↓					↓	[117]
						Pot	↓	↓	↓				↓					↑	[109]
						Pot	↓		↓				↓	↑	↑	↓	↑		[121]
						Pot	↓	↓		↓	↓	↓	↓	↑	↑	↓	↑	↑	[128]
						Pot	↓	↓	↓		↓	↓	↓	↑	↑	↓	↓	↑	[110]
						Pot	↓	↓	↓		↓	↓	↓	↑	↑	↓	↓	↓	[115]
						Pot	↓	↓					↓	↓	↓	↓	↓	↓	[115]

448 displayed thinner leaves under stress [113]. Leaf thickness has previously been suggested to be a  
 449 reliable indicator of a plant’s water status and stress level, with thinner leaves reducing water loss.

450 Brenes et al. [110] reported the maintenance of leaf relative water content (LRWC) in *S. insanum*  
 451 up to 300 mM NaCl while *S. melongena* LRWC was reduced after 100 mM NaCl. A reduction in  
 452 LRWC was also noted in two tomato cultivars [118], alongside reports of a reduction in water use  
 453 efficiency in *S. lycopersicum* [111, 119]. A change in water status has also been observed regarding  
 454 the leaf osmotic pressure in both *S. lycopersicum* and *S. chilense* which decreased under stress,  
 455 enabling osmotic adjustments to limit ion accumulation as a short-term tolerance strategy [117,  
 456 120]. A reduction in leaf osmotic pressure was, however, only observed in the most sensitive *S.*  
 457 *melongena* accessions while tolerant ones maintain it under stress, suggesting other mechanisms in  
 458 place for long-term tolerance [121]. Indeed, the long-term reduction in osmotic pressure can lead to  
 459 negative changes in various parameters such as cell membrane stability, which was reduced in every  
 460 tomato accession tested under salinity by Ahsan et al. [122] and in *S. melongena* [123].

461 Variations in leaf morphology and water content can, in turn, affect chlorophyll levels. Doganlar,  
 462 Demir, Basak, and Gul [124] showed that chlorophyll was affected very early on with changes already  
 463 seen 24 h after the start of salinity stress in *S. lycopersicum*. At the end of salinity stress, a range  
 464 of studies on *Solanum* has reported no or little effects on total chlorophyll under salinity while  
 465 carotenoids were more often reduced, suggesting a potential shift in light-harvesting wavelengths  
 466 throughout the stress [110, 115, 116]. Photosynthesis activity can eventually be affected due to a  
 467 combination of affected pathways including light harvesting changes. Liao and Zhang [125] reported  
 468 a gradual decrease in assimilation rate, stomatal conductance, and intracellular CO<sub>2</sub> in *S. nigrum*  
 469 as the salinity level increased. Similarly, a reduction in net photosynthesis rate and stomatal  
 470 conductance was observed in *S. lycopersicum* [116, 126], *S. melongena* and *S. nigrum* [110]. In  
 471 addition, non-photochemical quenching, representing the amount of light dissipated as heat by the  
 472 plant to avoid photodamage via the production of reactive oxygen species (ROS), was increased in

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473 the brinjal eggplant and tomato [127, 128]. Despite this increase, ROS  $\text{H}_2\text{O}_2$  and  $\text{O}_2^-$  were still  
474 recorded in high levels in these crops [127, 128]. While this was observed by Li et al. [129] for  $\text{O}_2^-$ ,  
475 the increase of  $\text{H}_2\text{O}_2$  is less consistent with some reports of no salinity effects [109, 115]. When  
476 comparing  $\text{H}_2\text{O}_2$  levels in potato leaf, stem, and root, Jaarsma, Vries, and Boer [130] showed that  
477 leaf levels were unchanged in most accessions but stem and root  $\text{H}_2\text{O}_2$  were highly increased under  
478 salinity, highlighting plant organ differences in stress marker accumulation and explaining in part  
479 the variability of the observations previously made.

480 Ion accumulation within plants under salinity is broadly accepted with the increase of sodium  
481 ions and decrease of the potassium over sodium ratio in various plant parts [131]. This disruption  
482 causes secondary negative effects with damages to the cell membrane and various enzymes [131].  
483 Albaladejo, Meco, Plasencia, Flores, Bolarin, and Egea [113] noted a clear sodium increase in roots  
484 and leaves of *S. pennellii* and *S. lycopersicum* under salinity with *S. pennellii*, more tolerant than *S.*  
485 *lycopersicum*, showing a less drastic leaf uptake. This clear increase was also noted in *S. melongena*  
486 and *S. insanum* alongside an increase in chloride ions [110, 123]. A range of secondary metabolites  
487 is produced in response to this stress including osmolytes such as proline, glycine betaine or sugars,  
488 which help maintain a low osmotic potential [132]. Fruit sugars have been reported to be increased  
489 under salinity in eggplant and tomato, but not in *S. chilense*, considered the most tolerant species  
490 among those [123, 133]. *S. insanum*, a more tolerant species, accumulated proline and sugars to a  
491 higher level than *S. melongena* under stress [110]. These osmolytes and their localisation seem thus  
492 to be important in plants' tolerance to salinity by acting as signalling molecules but also directly  
493 protecting cells from the damaging effects of ion accumulation, for example [132].

494 Changes in ROS level under salinity trigger an antioxidant response by crops, as observed by  
495 the effect on antioxidant enzymes in potato [134], tomato [128], brinjal eggplant [123] and *S. nigrum*  
496 [125]. The antioxidant response can affect greatly crop tolerance as was seen in *S. tuberosum* where  
497 the most tolerant cultivar showed an increase in ascorbate peroxidase and glutathione reductase  
498 in the shoot that was not observed in the sensitive accession [135]. Ahanger, Mir, Alyemini, and  
499 Ahmad [128] reported an increase in all antioxidant enzymes measured, total flavonoids and phenols  
500 in tomato, with the latter also increased in eggplant fruits and tomato leaves in other studies [123,  
501 126]. This antioxidant response seems to be triggered at low salinity levels as shown by Ben  
502 Abdallah et al. [109] who demonstrated that phenols increased at 50 mM NaCl. Surprisingly, a  
503 higher level of salinity removed this effect with no increase or decrease noted at 100 and 150 mM  
504 NaCl compared to no salinity [109]. In the same vein, *S. villosum* and *S. insanum* only showed  
505 changes in phenols and flavonoids at medium salinity levels while no differences were noted between  
506 non-stressed plants and plants watered with a 150 mM NaCl solution [110, 136]. In some studies,  
507 no effects were noted at all [110, 133]. These differences suggest a complex link between stress and  
508 antioxidant responses, heavily reliant on the stress intensity with other mechanisms in place when  
509 the salinity level is high. Plant age might also be a factor in the observed antioxidant responses  
510 as supported by Djanaguiraman and Prasad [131], with older plants showing fewer variations of  
511 antioxidant levels.

### 512 3.4 Stress combination

513 Exploring the effects of stress combination is of utmost importance to understand how crops will  
514 react in natural conditions in current and future agricultural settings. Drought is often associated  
515 with high temperatures while high temperatures can increase soil salinity by reducing the soil  
516 leaching capacity for example [6]. While responses to individual stresses have been extensively  
517 studied as seen above, especially in model crops, stress combination is only starting to be researched.  
518 Crops can respond to stress combinations by showing completely new responses, the addition of  
519 individual stress, or the effects of only one of the stress when this stress is predominant [137]. Heat  
520 and drought and a few other stress combinations on *Solanum* are discussed below.

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### 521 3.4.1 Heat and drought

522 Plant development was reduced by the combination of heat and stress to a lower level than the  
523 reduction observed under each stress in both *S. lycopersicum* and *S. melongena* [97, 138, 139].  
524 In a study by Francesca et al. [140], the growth of plants under the combination of heat and  
525 drought was reduced to the same level as when under drought alone, despite the enhancement of  
526 vegetative growth by heat, also observed by Duan et al. [88]. The positive effect of heat seems thus  
527 to not be compensating for the highly damaging effects of drought. The same trend was observed  
528 for chlorophyll pigments with a decrease under the stress combination despite an increase under  
529 drought, mostly due to the decrease under heat [86, 88]. When both heat and drought reduced  
530 chlorophyll levels individually, their combination seems to show an additive effect with a further  
531 reduction reported [97].

532 Stomatal conductance followed the same trend, with an increase under heat but an overall  
533 reduction to the drought-stressed plants' levels when both stresses were present in combination [86,  
534 88, 140]. Overall photosynthesis was, however, generally further decreased by the stress combination  
535 [86, 97, 138]. Tomato plants grown at 45° C without irrigation, for example, had a more severe  
536 effect on photosynthesis and biochemical stress markers than the individual temperature increase  
537 and irrigation withdrawal [99]. Under a less intense heat treatment reaching 32°C combined with  
538 no irrigation, plants mostly displayed characteristics of drought alone [60]. These results suggest  
539 a complex interaction of the stresses depending on their intensity and length which will determine  
540 the mechanisms put in place by the plants to withstand stress.

541 H<sub>2</sub>O<sub>2</sub> and MDA were further increased under stress combination, suggesting a stronger oxidative  
542 stress response [97, 138]. This was not matched by a further increase in antioxidant enzyme activity  
543 in either study, suggesting a plateau already reached under individual stresses or the triggering of  
544 other pathways instead to control the increase in damaging compounds [97, 138]. Hannachi, Signore,  
545 Adnan, and Mechi [97] reported stress hormones to be increased to the same levels as observed  
546 under drought alone while Francesca et al. [140] observed this in sugars, following the same trend as  
547 antioxidant enzymes. Despite an additive effect in some growth parameters, a range of commonly  
548 measured characteristics seems to not be further exacerbated by the stress combination, especially  
549 when focusing on secondary metabolites.

### 550 3.4.2 Salinity and drought

551 Unlike the combination of heat and drought, plant growth was only more affected by the combination  
552 of drought and salinity when salinity was present at a high level [141]. Before that, drought  
553 was predominant over salinity. In the same study, photosynthesis activity was also not further  
554 impacted by drought and salinity combination with a decrease to the same extent as the decrease  
555 observed under individual stresses [141]. In another study when both stresses were more intense, the  
556 combination of drought and salinity led to a lower leaf water potential, higher sodium accumulation  
557 and increased proline response [142]. This was further confirmed by leaf fluorescence measurements,  
558 supporting the importance of stress length and intensity when talking about tolerance and resistance  
559 [142]. A study in tomato plants by Ors, Ekinici, Yildirim, Sahin, Turan, and Dursun [143] showed  
560 that salinity reduced the drought threshold needed before negative effects on CO<sub>2</sub> assimilation  
561 and mineral concentrations were observed. Understanding this interaction is thus crucial as  
562 monitored water deficit treatment following guidelines based on the application of water stress  
563 alone is sometimes used to improve fruit quality [144]. The presence of another stress might lead  
564 to unwanted effects such as reduced growth and final yield depending on the combined intensity.

### 565 3.4.3 Salinity and heat

566 In a study investigating heat and salinity, sodium transport rate was reduced under the stress  
567 combination when compared to salinity alone, potentially reducing the negative effects of ion

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568 accumulation observed under salinity [145]. The high temperature also had a protective effect on  
569 the photosynthetic activity of plants under salinity with a reduction of the defects under the stress  
570 combination when compared to salinity on its own [145]. This was further observed by Lopez-  
571 Delacalle, Silva, Mestre, Martinez, Blanco-Ulate, and Rivero [146] which showed the recovery of  
572 assimilation rate when heat was present alongside salinity while a significant drop was noticed  
573 under salinity alone. These positive interactions are, however, not observed every time. Sousa  
574 et al. [147], using a 7°C higher temperature than the research presented previously, showed an 8%  
575 increase in shoot sodium accumulation under heat and salinity when compared to salinity alone.  
576 The stress combination also reduced shoot calcium despite an increase under both salinity and heat  
577 individually [147]. In another study, the highest decrease in photosynthetic activity was observed  
578 under the combination of stresses [148]. Similarly, heat protection was not observed on yield in a  
579 separate study, showing limitations to the positive interactive effect, especially when salinity levels  
580 are low [149]. The stress combination also impacted plant metabolites differently than individual  
581 stresses with sugars and some acids being further increased by their interaction in the study by  
582 Botella et al. [149] and antioxidants being regulated differently in the study of García-Martí et al.  
583 [148].

584 The variability of results previously observed within the *Solanum* kingdom under drought, heat,  
585 salinity and their combination highlight the need to investigate the African eggplant responses to  
586 get a better understanding of its role in stressed environments. The potential beneficial effect of  
587 some stress combinations such as heat and salinity is important to investigate to understand new  
588 possibilities in future food systems.

## 589 4 Improving stress tolerance with biostimulants

590 A range of reviews tackles the long-term crop improvements through breeding [150, 151]. In this  
591 part of the review, the focus will be on biostimulants as a short-term solution for farmers.

592 To strengthen plant stress response mechanisms, the use of biostimulants has been employed  
593 in multiple cases in pot or field conditions. Biostimulants are described as "substance(s) and/or  
594 micro-organisms whose action when applied to plants or the rhizosphere is to stimulate natural  
595 processes to enhance/benefit nutrient uptake, nutrient efficiency, tolerance to abiotic stress, and  
596 crop quality" according to the European Biostimulants Industry Council [152]. Their application  
597 is an environmentally friendly method to enhance crop performance and the quality of the edible  
598 product, used mostly on high-value crops such as vegetables [153, 154]. They can be categorised as  
599 follow [155]:

- 600 • Humic and fulvic acids, originating from dead organic matter [156]
- 601 • Protein hydrolysates and other N-containing compounds [157]
- 602 • Seaweed extracts and botanicals [158]
- 603 • Chitosan and biopolymers, mainly derived from crustacean shells [159]
- 604 • Inorganic compounds [160]
- 605 • Microbial compounds [161]

606 Biostimulants have been shown to have beneficial effects mostly when crops are under stress  
607 conditions [7]. Under optimal conditions, the use of biostimulants does not tend to improve plant  
608 growth or nutritional quality, making them redundant. Hernández-Herrera, Santacruz-Ruvalcaba,  
609 Ruiz-López, Norrie, and Hernández-Carmona [162] even showed that some seaweed extracts slowed  
610 down germination and limited seedling growth in tomato under non-stressed conditions. Under  
611 drought, the levels of enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT),  
612 and peroxidase (POD) increased in stressed plants treated with a biostimulant before or after the

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613 stress [163–165]. Yield parameters, including biomass, fruit production, and fresh and dry weight  
614 of the plant, also increased in treated plants under drought [166–168]. In tomatoes grown under  
615 heat stress, fruit set and development have been improved with the use of biostimulants [169],  
616 as has the activity of SOD, CAT, and POD [170], and stomatal conductance and photosynthetic  
617 assimilation rate [171]. Tomatoes grown under salinity reported an increase in leaf area [172],  
618 biomass production [173], and yield [174] when treated with biostimulants. Fruit quality was also  
619 enhanced by biostimulants with an increase in antioxidants, total soluble sugars, and minerals  
620 [175–177]. The effect of biostimulants can fluctuate, however, with some reports of no or small  
621 effects. The success of biostimulants depends on a variety of factors, such as the timing and  
622 method of application, stress and cultivar studied, or growth stages [7]. Their combination seems  
623 particularly promising [178]. The *one-size-fits-all* approach is not appropriate for biostimulant use  
624 and research on particular conditions is needed to provide farmers with efficient methods of coping  
625 with environmental stresses now.

## 626 5 Conclusions

627 The constant environmental stresses faced by farmers negatively impact yields, crop nutritional  
628 quality, and overall plant development. The interplay of stresses, often observed in the field, adds  
629 a level of complexity when predicting the effects of these stresses on our food systems. *Solanum*  
630 *aethiopicum* is an indigenous crop with a high potential to ensure the sustainability and resilience  
631 of food systems in Africa due, in part, to its high genetic variability. Research on the stress  
632 tolerance of *S. aethiopicum* is sparse, especially on heat and salinity, despite some knowledge based  
633 on its evolutionary path. Investigating its unique responses to a range of environmental stresses  
634 individually or in combination, alongside its interaction with biostimulants when needed, is key to  
635 helping fight food insecurity and crop diversity decline.

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