Review Article

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

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 reviews 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

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

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

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

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

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

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

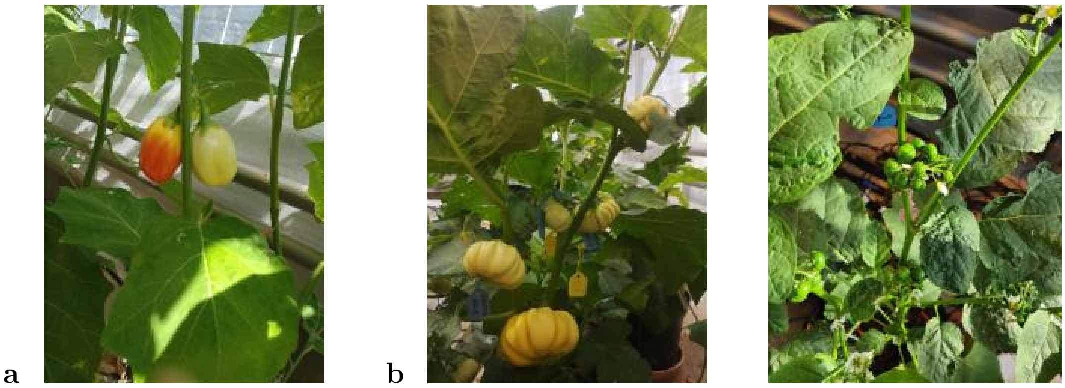


Figure 1: African eggplant **(a)** Gilo, cv. DB3 **(b)** Kumba, cv. Mekevan **(c)** Shum, cv. E11 grown at NIAB East Malling, UK.

2.2 Cultivation

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

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

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

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

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

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

2.3 Distribution and use

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

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

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

2.4 Nutritional and pharmaceutical properties

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

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

2.5 Breeding and genetic resources

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

A major part of the currently grown varieties is a result of farmers' selection based on their or the consumers' preferences. Nevertheless, 98% of the commercial seeds in East and Southern Africa in 2014 were improved varieties developed by the World Vegetable Centre (WVC) [42]. This number does not translate to the most commonly grown varieties yet as most farmers will use their own seeds rather than the commercial ones, as stated above. WVC has been working on African eggplant varieties since 1993 and released multiple cultivars, such as the highly popular gilo cultivar in Tanzania in 2006 called DB3 [43]. In 2016, the WVC selected the African eggplant as a major strategic crop for breeding based on its importance in African countries, nutritional value and income generation potential [12]. There is a high genetic diversity for the African eggplant with 798 genebank accessions conserved worldwide, 481 by the WVC [18]. Farmers across Africa keep a large genetic resource as each region seems to have a preference for different morphological traits and is thus cultivating their own local varieties of African eggplant [17]. As the same variety cultivated in different regions can have a different name, recording the actual diversity is sometimes a challenge [28].

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

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

3 Abiotic stress in *Solanum*

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

3.1 Drought

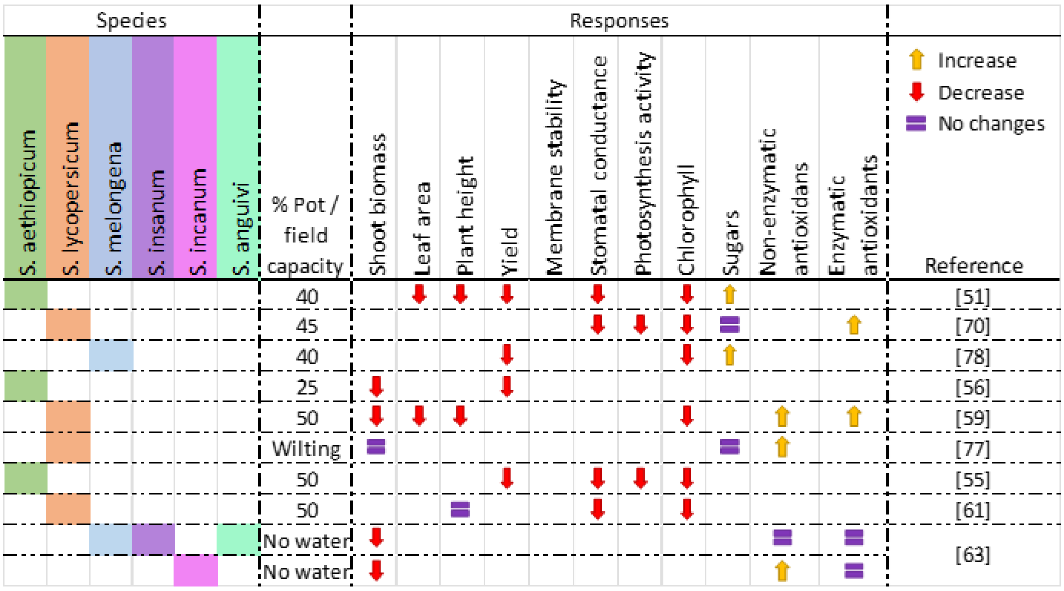
Drought stress is one of the most damaging factors in crop production with effects on plants' morphology, physiology, and biochemical processes [50]. Table 1 depicts graphically some of the literature available on drought effects on *Solanum* species.

3.1.1 *Solanum aethiopicum* under drought

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

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



⬆ Increase
⬇ Decrease
= No changes

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

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

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

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

3.1.2 *Solanum* species under drought

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

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

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

A decrease in water status is a signal for plants to close their stomata in order to limit further water loss through transpiration [50]. This closure was noted in tomato even at a low-stress level of 15% irrigation reduction and at every growth stage [60, 61, 68, 70]. Stomatal closure has been generally said to be the main driver for decreased photosynthesis under drought, eventually leading to reduced fruit production. Other mechanisms can, however, decrease photosynthesis following drought as well due to the complex photosynthetic mechanisms. For example, drought often leads to a reduction in chlorophyll production as reported in *S. melongena* [71] and *S. lycopersicum* [72], eventually reducing the light-harvesting capacity of the plants. In a study by Çelik, Ayan, and Atak [68] in tomato, leaf photosynthetic pigments were reduced two days after the beginning of stress, showing a dynamic and fast process. A chlorophyll decrease in tomato was most prevalent during the vegetative stage, when sufficient photosynthesis activity is crucial to develop resources to start flowering, and at fruit set [61]. Nonetheless, chlorophyll can also increase in some cultivars under water stress as seen in eggplants by the study of Mahammed, Babu, Lakshmana, Ganapathi M, and Rakshith [73]. This increase, measured per leaf area, can be due to the smaller leaves observed under drought, leading to a higher concentration of chlorophyll per area but can also be an intrinsic mechanism to enhance light harvest while limiting water loss. Alongside photosynthesis pigments, membrane stability is crucial to maintain photosynthesis activity [50]. Under drought, membrane stability, measured by the amount of electrolyte leakage, has regularly been reported to increase proportionally to the level of stress in eggplant and tomato [73, 74]. Leakage of electrolytes has often been related to photosynthetic and mitochondrial activity reductions in plants.

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

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

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

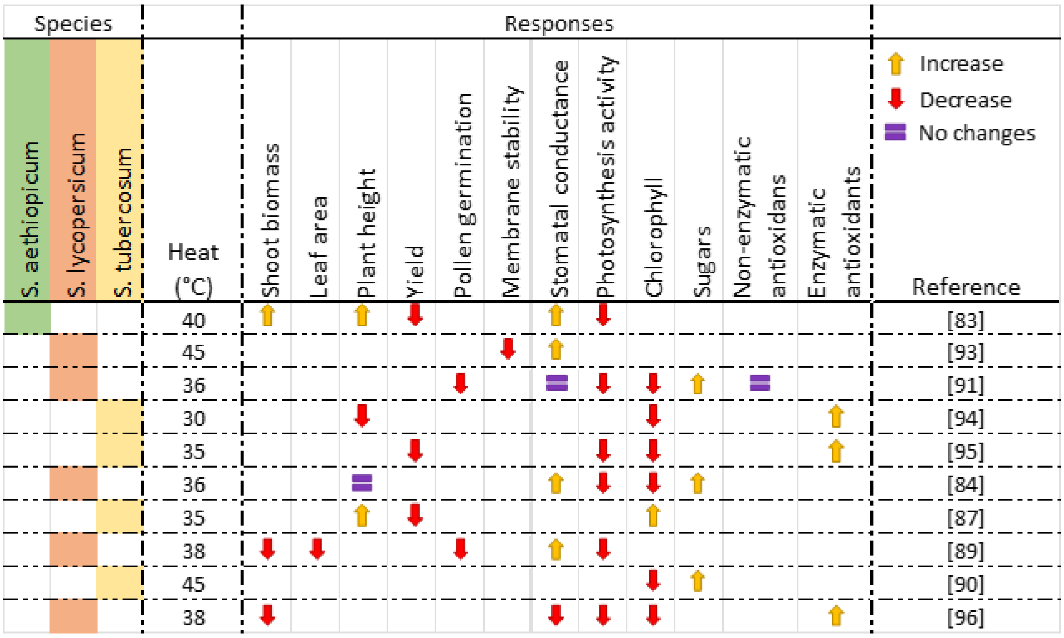
3.2 Heat

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

3.2.1 *Solanum aethiopicum* under heat

S. aethiopicum L. cv. Legon Prolific, a gilo cultivar, has been shown to have an increased photosynthesis activity and stomatal conductance between 30°C and 35°C but decreased at 40° 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												
S. aethiopicum	S. lycopersicum	S. tubercosum	Heat (°C)	Shoot biomass	Leaf area	Plant height	Yield	Pollen germination	Membrane stability	Stomatal conductance	Photosynthesis activity	Chlorophyll	Sugars	Non-enzymatic antioxidans	Enzymatic antioxidants	Reference
🟩			40	⇧		⇧	⬇			⇧	⬇					[83]
	🟧		45						⬇	⇧						[93]
	🟧		36					⬇		=	⬇	⬇	⇧	=		[91]
		🟨	30			⬇						⬇			⇧	[94]
		🟨	35				⬇				⬇	⬇			⇧	[95]
	🟧		36			=				⇧	⬇	⬇	⇧			[84]
		🟨	35			⇧	⬇					⇧				[87]
	🟧		38	⬇	⬇			⬇		⇧	⬇					[89]
		🟨	45									⬇	⇧			[90]
	🟧		38	⬇						⬇	⬇	⬇			⇧	[96]

⇧ Increase
⬇ Decrease
= No changes

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

3.2.2 *Solanum* species under heat

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

Leaf production and development are, in general, hindered at high temperatures as seen in both tolerant and sensitive tomato cultivars [89] and potato [90] after a certain threshold. No change in leaf number was noted, however, in young tomatoes grown at 36°C and leaves produced were the same size in another study growing tomatoes at 40°C [84, 85]. The different growth stages and stress lengths, with the latter studies focusing on short-term stress at early stages, might explain these antagonist effects observed. Under heat stress, smaller leaves are a way to limit excess transpiration and water loss.

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

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

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

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

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

3.3 Salinity

Saline soils contain excessive soluble salts, mainly sodium chloride (NaCl) and sodium sulphate (Na_2SO_4), and are generally described as having an electrical conductivity higher than 4 dS/m [105]. This represented 412 million hectares of soil in 2015, 122.9 of which in Africa [105]. Different salinity intensities are further defined as seen in Table 3. Salinity disturbs every growth stage of crops, especially during seedling development, via osmotic or ion-excess responses [106]. The former is due to the lower uptake of water by the plant due to the high salt concentration in soil and has a rapid onset, while the latter is caused by the excessive uptake of Na^+ and Cl^- over a long exposure period. A range of processes is affected by salinity in Solanaceous crops including morphological, physiological and molecular pathways [107]. Table 4 depicts graphically some of the literature available on salinity effects on *Solanum* species.

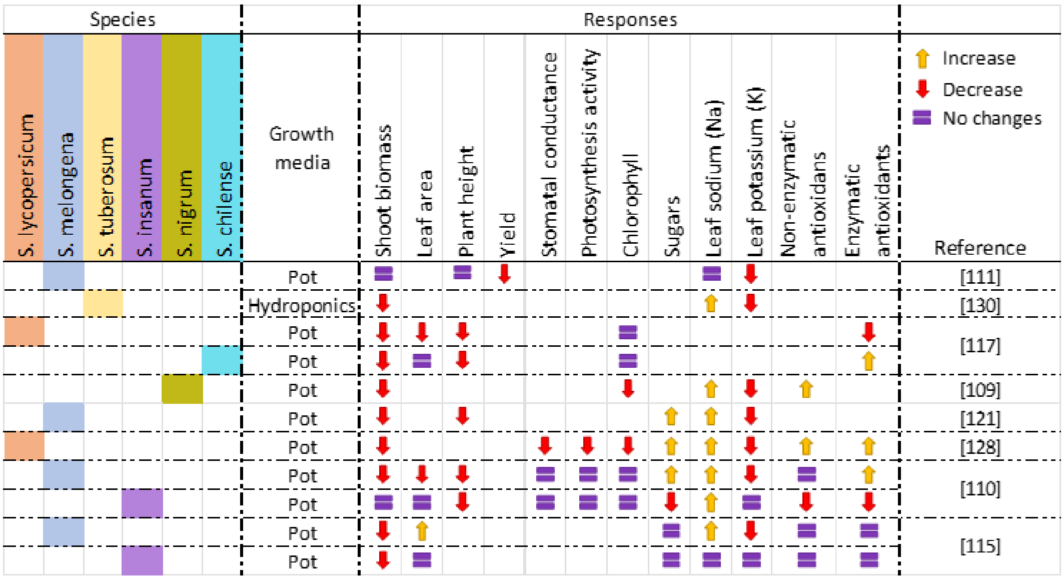
Table 3: Soil salinity classes in electrical conductivity EC_e

Salinity rating	Non-saline	Weakly saline	Moderately saline	Strongly saline	Very strongly saline
EC_e (dS/m)	< 2	2 - 4	4 - 8	8 - 16	> 16

3.3.1 *Solanum* species under salinity

Salinity stress affects *Solanum* species from the germination stage, with both *S. lycopersicum* and its close relative *S. nigrum* displaying reduced seed germination under NaCl irrigation, even if the wild *S. nigrum* was less affected [108]. Of the germinated seeds, both root and shoot growths were limited by the stress [108]. This negative effect on root and shoot was also observed in the plants' vegetative stages [109, 110]. Interestingly, even high levels of salt did not reduce plant growth parameters in *S. insanum*, a wild ancestor of the brinjal eggplant, highlighting the tolerance potential of *Solanum* species [110]. Another study showed a reduction in final yield but no signs of stem diameter or root length defects on the brinjal eggplant under high salinity levels, showing variations between accessions and stress length [111]. In *S. melongena*, root growth was even promoted under salinity and stem and leaf development was maintained, even though this was not sufficient to maintain final yield [112]. *S. pennelli*, a salt-tolerant crop, formed the central focus of a study by Albaladejo, Meco, Plasencia, Flores, Bolarin, and Egea [113] in which the authors found a slow tolerance mechanism. When compared to *S. lycopersicum*, shoot and root growth rate was much slower in the tolerant crop than in tomato after seven days of stress, but this was reversed after 14 days [113]. Due to the two-step toxicity mechanism of salinity, tolerance can take place at different stages and might only be perceived when a threshold is passed. Growth stages also seem to affect greatly how plants react to salinity stress with an increased tolerance at later stages [114]. Leaf development was reduced in *S. melongena* at lower salinity levels than stem or root development, showing differences between plant organs [110]. This decrease in leaf production was also observed in *S. nigrum* [109], *S. insanum* [115], *S. lycopersicum* [116] and *S. chilense* [117]. 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											
S. lycopersicum	S. melongena	S. tuberosum	S. insanum	S. nigrum	S. chilense	Growth media	Shoot biomass	Leaf area	Plant height	Yield	Stomatal conductance	Photosynthesis activity	Chlorophyll	Sugars	Leaf sodium (Na)	Leaf potassium (K)	Non-enzymatic antioxidans	Enzymatic antioxidants	Reference
	■					Pot	=		=	↓					=	↓			[111]
		■				Hydroponics	↓								↑	↓			[130]
■						Pot	↓	↓	↓				=					↓	[117]
					■	Pot	↓	=	↓				=					↑	
				■		Pot	↓						↓		↑	↓	↑		[109]
	■					Pot	↓		↓					↑	↑	↓			[121]
■						Pot	↓				↓	↓	↓	↑	↑	↓	↑	↑	[128]
	■					Pot	↓	↓	↓		=	=	=	↑	↑	↓	=	↑	[110]
			■			Pot	=	=	↓		=	=	=	↓	↑	=	↓	↓	
	■					Pot	↓	↑						=	↑	↓	=	=	[115]
			■			Pot	↓	=						=	=	=	=	=	

↑ Increase
↓ Decrease
= No changes

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

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

Variations in leaf morphology and water content can, in turn, affect chlorophyll levels. Doganlar, Demir, Basak, and Gul [124] showed that chlorophyll was affected very early on with changes already seen 24 h after the start of salinity stress in *S. lycopersicum.* At the end of salinity stress, a range of studies on *Solanum* has reported no or little effects on total chlorophyll under salinity while carotenoids were more often reduced, suggesting a potential shift in light-harvesting wavelengths throughout the stress [110, 115, 116]. Photosynthesis activity can eventually be affected due to a combination of affected pathways including light harvesting changes. Liao and Zhang [125] reported a gradual decrease in assimilation rate, stomatal conductance, and intracellular CO_2 in *S. nigrum* as the salinity level increased. Similarly, a reduction in net photosynthesis rate and stomatal conductance was observed in *S. lycopersicum* [116, 126], *S. melongena* and *S. nigrum* [110]. In addition, non-photochemical quenching, representing the amount of light dissipated as heat by the plant to avoid photodamage via the production of reactive oxygen species (ROS), was increased in the brinjal eggplant and tomato [127, 128]. Despite this increase, ROS H_2O_2 and O_2^- were still recorded in high levels in these crops [127, 128]. While this was observed by Li et al. [129] for O_2^-, the increase of H_2O_2 is less consistent with some reports of no salinity effects [109, 115]. When comparing H_2O_2 levels in potato leaf, stem, and root, Jaarsma, Vries, and Boer [130] showed that leaf levels were unchanged in most accessions but stem and root H_2O_2 were highly increased under salinity, highlighting plant organ differences in stress marker accumulation and explaining in part the variability of the observations previously made.

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

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

3.4 Stress combination

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

3.4.1 Heat and drought

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

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

H_2O_2 and MDA were further increased under stress combination, suggesting a stronger oxidative stress response [97, 138]. This was not matched by a further increase in antioxidant enzyme activity in either study, suggesting a plateau already reached under individual stresses or the triggering of other pathways instead to control the increase in damaging compounds [97, 138]. Hannachi, Signore, Adnan, and Mechi [97] reported stress hormones to be increased to the same levels as observed under drought alone while Francesca et al. [140] observed this in sugars, following the same trend as antioxidant enzymes. Despite an additive effect in some growth parameters, a range of commonly measured characteristics seems to not be further exacerbated by the stress combination, especially when focusing on secondary metabolites.

3.4.2 Salinity and drought

Unlike the combination of heat and drought, plant growth was only more affected by the combination of drought and salinity when salinity was present at a high level [141]. Before that, drought was predominant over salinity. In the same study, photosynthesis activity was also not further impacted by drought and salinity combination with a decrease to the same extent as the decrease observed under individual stresses [141]. In another study when both stresses were more intense, the combination of drought and salinity led to a lower leaf water potential, higher sodium accumulation and increased proline response [142]. This was further confirmed by leaf fluorescence measurements, supporting the importance of stress length and intensity when talking about tolerance and resistance [142]. A study in tomato plants by Ors, Ekinci, Yildirim, Sahin, Turan, and Dursun [143] showed that salinity reduced the drought threshold needed before negative effects on CO_2 assimilation and mineral concentrations were observed. Understanding this interaction is thus crucial as monitored water deficit treatment following guidelines based on the application of water stress alone is sometimes used to improve fruit quality [144]. The presence of another stress might lead to unwanted effects such as reduced growth and final yield depending on the combined intensity.

3.4.3 Salinity and heat

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

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

4 Improving stress tolerance with biostimulants

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

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

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

Biostimulants have been shown to have beneficial effects mostly when crops are under stress conditions [7]. Under optimal conditions, the use of biostimulants does not tend to improve plant growth or nutritional quality, making them redundant. Hernández-Herrera, Santacruz-Ruvalcaba, Ruiz-López, Norrie, and Hernández-Carmona [162] even showed that some seaweed extracts slowed down germination and limited seedling growth in tomato under non-stressed conditions. Under drought, the levels of enzymatic antioxidants such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD) increased in stressed plants treated with a biostimulant before or after the stress [163–165]. Yield parameters, including biomass, fruit production, and fresh and dry weight of the plant, also increased in treated plants under drought [166–168]. In tomatoes grown under heat stress, fruit set and development have been improved with the use of biostimulants [169], as has the activity of SOD, CAT, and POD [170], and stomatal conductance and photosynthetic assimilation rate [171]. Tomatoes grown under salinity reported an increase in leaf area [172], biomass production [173], and yield [174] when treated with biostimulants. Fruit quality was also enhanced by biostimulants with an increase in antioxidants, total soluble sugars, and minerals [175–177]. The effect of biostimulants can fluctuate, however, with some reports of no or small effects. The success of biostimulants depends on a variety of factors, such as the timing and method of application, stress and cultivar studied, or growth stages [7]. Their combination seems particularly promising [178]. The *one-size-fits-all* approach is not appropriate for biostimulant use and research on particular conditions is needed to provide farmers with efficient methods of coping with environmental stresses now.

5 Conclusions

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

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