Solanum crops with a focus on the African eggplant: the potential of biostimulants to enhance stress tolerance.

Review paper

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 status 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 to enhance stress tolerance are also discussed for each stress and their combination.

Keywords: African eggplant, 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 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 reducing leaf production, photosynthesis, and yield [4]. When stress is detected, crops activate a range of responses to survive, which depends on the stress intensity, length, and cultivar involved [4]. Despite some common responses to stress, such as the production of reactive oxygen species (ROS) 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 responses by plants not observed under individual stress, adding to the complexity of predicting how current plants will cope in the future [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, especially when used in combination [7]. 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 [8]. Their application is an environmentally friendly method to enhance crop performance and quality, used mostly on high-value crops such as vegetables [9, 10].

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 [11]. Innovative ways to ensure sustainable and resilient farming are thus needed to ensure food security and reduce poverty. While the Green Revolution was key to improving the yield of grains and staple food, malnutrition is increasing in all parts of the world [12]. While grains are important to reducing famine, vegetables are key to tackling malnutrition due to their high levels of nutrients and vitamins. Under-used vegetables, such as indigenous vegetables (IVs), are of particular importance due to the broad genetic pool they offer for breeding purposes [13]. Indigenous vegetables are widespread in Africa, a source of biodiversity, and adapted to local conditions, often displaying tolerance to environmental stresses [14]. Many IVs are nutrient-rich and part of local markets, hence could support and strengthen current agricultural systems to deliver sustainable diets regarding human nutrition and environmental issues [15]. The use of IVs to increase field resilience through crop diversity has been limited to date due to the lack of interest and investment [16]. They are under-researched and not used to their full potential, thus not as competitive as main crops such as maize, wheat, or tomato [16]. The indigenous vegetable market opportunities are still restricted and the combination of low yields and variable prices due to the locality of products are adding to their limited usage [17]. Indigenous vegetables include the African eggplant (*Solanum aethiopicum*), Ethiopian mustard (*Brassica carinata*), okra (*Abelmoschus esculentus*), and legumes such as cowpea (*Vigna unguiculata*), and Bambara groundnut (*Vigna subterranea*) [14, 18]. The African eggplant, also referred to as scarlet eggplant, has received increasing scientific attention due to its high nutritional value, taxon diversity, and market presence in a number of countries [19]. 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 [20]. This review highlights the latest research on the African eggplant, reviews the effects of drought, heat and salinity on *Solanum* crops, in particular the African eggplant, and investigates some methods used to improve stress tolerance.

2 *Solanum aethiopicum*

2.1 Taxonomy and genetics

The African eggplant originates from Africa and has been domesticated from *S. anguivi*, still found in the wild [21]. It 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*) [22]. The African eggplant is a complex hermaphrodite species consisting of four groups distinct both morphologically and in their use: shum, gilo, kumba, and aculeatum [23, 24] (Fig 1).

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 [25]. Shum varieties are found in the higher rainfall zones of West and Central African countries, or grown in swamps during the dry season [21]. Due to the recurrent shoot and leaves harvest for selling, plants do not grow tall and will develop instead a much-branched architecture with weak stems and many small laves, preferred by the consumers [26].

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 [25]. They usually have one to three 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 [27]. Gilo plants grow well at a temperature between 25 and 35°C during the day and 20 to 27°C at night [23]. Due to gilo's higher morphological complexity than shum, it has been suggested that the former has 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 [25]. Plants from this group do not grow very tall, around 40 to 50 cm [27]. Nowadays, kumba varieties with hairy leaves and only grown for their fruits are preferred in some regions due to their increased tolerance to pests [27]. Kumba plants tolerate high temperatures up to 45°C during the day [23].

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

Finally, plants from the aculeatum group produce inedible fruits and leaves, mostly used as ornamentals, and are the least common group grown in Africa [25].

Each group is hypervariable with hundreds of local varieties across Africa [28]. 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 within the African eggplant species [29].

2.2 Cultivation

Seeds of fruity varieties of African eggplant are sold commercially by various seed producers. 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 [25].

Like many indigenous vegetables, the African eggplant is mostly grown by small-scale farmers [17]. It is a perennial crop but the yield is dramatically reduced after the first season. 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 growing 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 [30]. Even though the total production might be lower than in the rainy season, the market price of fruits produced during the dry season will be at its highest and the incidence of diseases and pests will be lowered. To promote growth and income stability, the African eggplant, highly shade-tolerant, is often intercropped with other crops such as amaranth or coconut [26].

Nitrogen and potassium are the most limiting nutrients in African eggplant growth [31]. 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 [30].

Leaf harvest from Shum varieties usually starts two months after sowing and can be repeated up to five times through one season [23]. 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 [23]. The earliest varieties belong to the kumba group and can be harvested at about 85 days from sowing while most types require 110 to 120 days. 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 [32]. Fruit weight can range from 25 to 110 g and yield varies significantly between areas, from 8.9 t/ha to more than 50 t/ha [18, 33]. Improved cultivars under favourable conditions have shown clear yield improvement reaching around 60 t/ha [34].

In addition to being cultivated for its fruits or leaves, the African eggplant 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 [35]. 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 [36].

2.3 Distribution and use

The African eggplant 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' [18, 23]. The fruit is consumed in East Africa while leaves are primarily consumed in Uganda and both leaves and fruits are eaten in West Africa [18]. Marketable fruits are creamy to green in colour, while red and ripe fruits are used to collect seeds but generally not eaten [18]. 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 [23]. 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 [23]. The highly bitter fruits of some cultivars, as well as the roots, are sometimes used as medicine to treat colic, high blood pressure or uterine complaints. Consumers are particularly attracted to the nutritional and medicinal value of the fruits and leaves.

The African eggplant fruit shelf-life extends from 3 to 7 days, leading to significant postharvest losses and drying the product has been suggested to counteract the waste produced [23]. Despite increasing shelf-life, drying methods reduce the pharmaceutical activity of the product and can be expensive, thus are still only sparsely used [37].

2.4 Nutritional and pharmaceutical properties

The African eggplant fruits have a high moisture content and very low caloric value and provide several fundamental mineral elements such as calcium, iron, zinc, and vitamins [38]. 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 [23]. Kumba plants tend to have the highest level of antioxidant activity while aculeatum plants 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 et al. [39] 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).

The African eggplant is used in traditional medicine to treat different conditions such as mental disorders or diabetes [40]. Due to the high antioxidant levels within the plant, they have been suggested to be used as nutraceutical supplements [41]. 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 [42], diabetes [43] and iron intake [44] 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 [45].

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 [46].

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) [47]. 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 DB3 in Tanzania in 2006 [18]. 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 [18]. There is a high genetic diversity for the African eggplant with 798 genebank accessions conserved worldwide, 481 by the WVC [24]. Farmers across Africa also 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 [23]. As the same variety cultivated in different regions can have a different name, recording the actual diversity is sometimes a challenge.

Some breeding programs for the African eggplant started already in the late 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 [23]. 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 sheds light on genes associated with disease resistance and drought tolerance [48]. 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 [49].

Since gene transfer between eggplant species is possible, the African eggplant is acknowledged as a source of variations in brinjal eggplant breeding [50]. This was shown early on by multiple studies which successfully introduced wilt resistance in the brinjal eggplant from the African eggplant [51, 52]. 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 et al. [53] 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 for breeding a stable increased performance under drought stress.

3 Abiotic stress in *Solanum* and the use of biostimulants

Abiotic stresses trigger some responses shared between plants, such as the activation of osmotic stress, but also lead to individual responses based on species, intensity, length, and developmental stage [4]. To strengthen plant stress response mechanisms and increase stress tolerance, biostimulants have been employed in multiple cases. They have been shown to have beneficial effects on plant viability mostly when crops are under stress [7]. Biostimulants can be categorised as follow [54]:

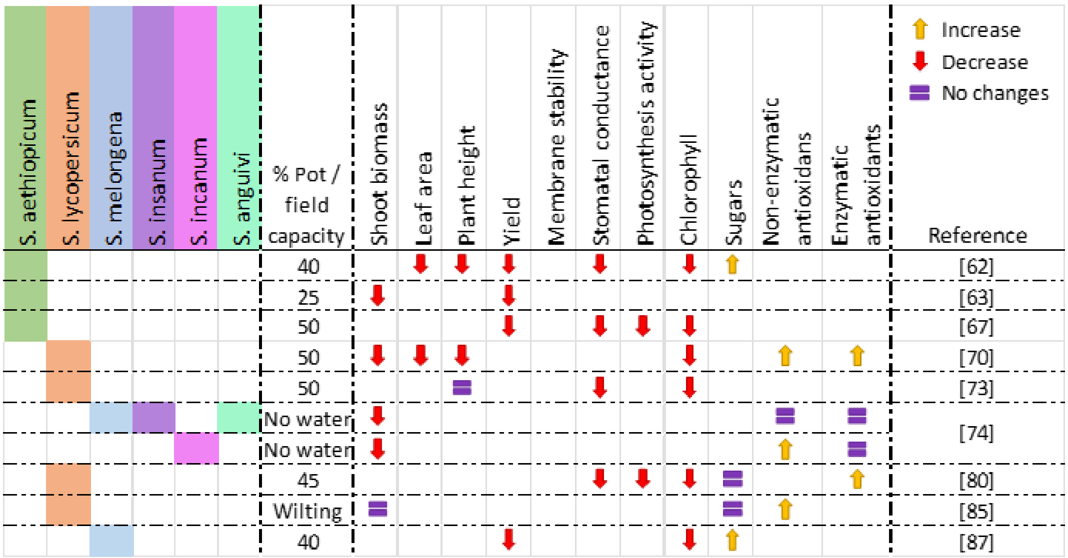
- Humic and fulvic acids, originating from dead organic matter [55]
- Protein hydrolysates and other N-containing compounds [56]
- Seaweed extracts and botanicals [57]
- Chitosan and biopolymers, mainly derived from crustacean shells [58]
- Inorganic compounds [59]
- Microbial compounds [60]

The effects of drought, heat, salinity and their combination on *Solanum* crops, focusing on *S. aethiopicum*, are explored below. Studies on the effects of biostimulants are also described for each stress.

3.1 Drought

Drought stress is one of the most damaging factors in crop production with effects on plants' morphology, physiology, and biochemical processes [61]. Table 1 depicts graphically some of the literature available on drought effects on *Solanum* species.

Table 1: Sub-sample of the available studies on the effect of drought on *Solanum* species. Each colour represents the *Solanum* species used in each study.



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		↓	↓	↓		↓		↓	↑			[62]
■						25	↓			↓								[63]
■						50				↓		↓	↓	↓				[67]
	■					50	↓	↓	↓					↓		↑	↑	[70]
	■					50			=			↓		↓				[73]
		■	■		■	No water	↓									=	=	[74]
				■		No water	↓									↑	=	
	■					45						↓	↓	↓	=		↑	[80]
	■					Wilting	=								=	↑		[85]
		■				40				↓				↓	↑			[87]

↑ Increase
↓ Decrease
= No changes

3.1.1 *Solanum aethiopicum* under drought

In a study by Lagat [62], a range of morphological and physiological aspects of the African eggplant were hindered 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% [62]. The variability observed, also observed in shum cultivars by Nakanwagi et al. [63], 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 [62]. These benefits were, however, counter-balanced by a decrease in mineral elements such as magnesium, calcium, iron and zinc, reducing the overall gain in fruits' nutritional quality [62].

Another study investigating drought effects on the African eggplant secondary metabolism also showed high variability between accessions [64]. Out of the 19 accessions tested, 10 displayed an increase in total carotenoids, 5 a decrease and 4 no change [64]. 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 neutraceutical carotenoids [64]. Further to their carotenoids study, Mibei et al. [65] 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 [65]. The authors shed light on important parts of the oxidative responses to drought in various accessions of the African eggplant and highlighted key metabolites involved in drought stress adaptation. The high diversity between accessions observed shows the great potential for tolerant species to be selected for farming.

When using one variety in the field, Mwinuka et al. [31] 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 at 50% irrigation reduction but not at 25%, highlighting a tolerance threshold [66]. 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 [67]. Photosynthesis and fruit yield, in opposition, were maintained at 75% pot capacity [67]. 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 [68]. This knowledge is important for farmers to ensure crop protection at key growing points.

The responses of the African eggplant 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 this crop due to the variability of results observed.

3.1.2 *Solanum* species under drought

Morphological defects caused by drought on *Solanum* can already be noticed at the seedlings stage with a reduced germination rate and seedling growth in eggplant under water stress [69]. A reduction of leaf area was noted in later stages in tomato by Kusvuran and Dasgan [70] with the maintenance of leaves number, suggesting the production of smaller leaves instead. This observation was also made by Zhou et al. [71] in two different cultivars, indicating an adaptive mechanism to limit water loss through leaf thinning. Fruit characteristics were also impacted in eggplant under drought with a reduction in diameter and length, reducing eventually marketable yield and profitability [72]. Even if drought impacts morphological characteristics at every growth stage, a study by Ghannem, Ben Aissa, and Majdoub [73] 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.

Root length was reduced in multiple tolerant and susceptible brinjal eggplant cultivars under no irrigation [74]. Root dry weight, however, was not reduced for tolerant cultivars in another study, showing diverse responses of root development by producing either larger roots or a higher number of small roots [74]. 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 thinner stems and reducing shoot dry weight overall, as observed in the brinjal eggplant [72] and tomato [75]. These reductions seem to only appear after a certain threshold with a reduction in irrigation by 20% or 25% not impacting significantly the brinjal eggplant development and yield, as seen by Mahmud et al. [76]. 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. A decrease in leaf relative water content (LRWC) has regularly been reported under drought and is now a common stress marker [77]. A reduced LRWC was noted in a drought-tolerant tomato cultivar, even though a sharper decrease was observed in a sensitive one [70]. This decrease is generally observed even at a low level of drought and at early stages but is quickly recovered after re-wetting the soil, highlighting the quick response of this marker [78]. 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 [61]. This closure was noted in tomato even at a low-stress level of 15% irrigation reduction and at every growth stage [71, 73, 77]. 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 due to the complex photosynthetic mechanisms. For example, drought often leads to a reduction in chlorophyll production, as reported in tomato [79, 80], eventually reducing the light-harvesting capacity of the plants. In a study by Çelik, Ayan, and Atak [77], 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 [73]. Nonetheless, chlorophyll can also increase in some cultivars under water stress as seen in the brinjal eggplant by the study of Mahammed et al. [81]. 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 [61]. Under drought, membrane stability, measured by the amount of electrolyte leakage, has regularly been reported to decrease proportionally to the level of stress [81, 82]. 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 [71]. Limited irrigation also increased non-photochemical quenching in the same study, showing an adaptive process to limit the creation of ROS produced due to the imbalance of the energy harvested and its utilisation [83]. Reactive oxygen species, 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 [84]. 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 [77]. Interestingly, levels of MDA were similar between tolerant and susceptible brinjal eggplant cultivars in a study by Plazas et al. [74], highlighting that MDA levels do not automatically translate to plant tolerance but can potentially trigger it.

In a study on one tomato cultivar, drought stress increased oxidative stress and enzymatic and non-enzymatic antioxidant levels as a response [79]. Lycopene, a major antioxidant in tomato, increased under stress in three cultivars alongside phenols, flavonoids, and total antioxidants [85]. Antioxidants are the main defenders to limit ROS damage and maintain cell processes [84]. When comparing susceptible, intermediate, and tolerant brinjal eggplant cultivars, Plazas et al. [74] 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 [74]. 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, phosphorus, and iron decreased in tomato already at 15% irrigation reduction, with further decreases noted when irrigation was withdrawn even more [86]. In the brinjal eggplant, however, a decrease of 20% irrigation did not impact nitrogen, potassium, or phosphorus, which were only reduced when irrigation was withdrawn by 60% or more [87]. *Solanum* nutrient uptake is thus different based on the species under drought, highlighting a potential genetic factor involved. This was observed in tomato cultivars where most cultivars had a reduction in their leaf nitrogen levels under drought except the tolerant ones [88]. 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 of enhancing selected mineral elements to maintain plant growth and photosynthetic activity [88].

3.1.3 Biostimulants to relieve drought stress

Biostimulants to enhance drought tolerance are successfully sold by a range of companies as a short-term and quick solution. When comparing a range of algae-based commercially available products, Goñi, Quille, and O'Connell [89] noted that despite differences in metabolites composition, all the products enhanced drought tolerance in tomato plants when looking at the final growth. These compounds had an effect on a range of parameters including proline and sugars levels, showing interaction with multiple processes [89]. Another commercial biostimulant used under drought helped tomato tolerance even though a decrease was still observed when compared to non-stressed plants, showing an incomplete recovery [90].

Photosynthesis activity was also recovered by the use of biostimulants made of algal extract and macro- and micronutrients, to a level even higher than that of non-stressed plants [91]. This study was performed at both flowering and fruiting stages, highlighting the non-specificity of these compounds in terms of growth stages. Final fruit production was also positively impacted, which is crucial to ensure the costs associated with these products are outweighed by the improved market potential [91].

Using protein hydrolysates, Paul et al. [92] showed an increased biomass production but no effects on most photosynthesis parameters tested. Tomato plants showed an increased tolerance to ROS damage though, supporting the previous results highlighting improvements in antioxidant enzymes to enhance tolerance [92]. The levels of enzymatic antioxidants superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), as well as germination parameters, increased in tomato plants treated with silicon at the same time as the stress occurred [93]. Silicon also increased shoot and root growth under drought-like stress and photosynthesis-related parameters in another study [94]. Despite the exact positive mechanisms of silicon-mediated tolerance not being fully defined, it is believed it helps with the plant water status and physiological processes [93]. These pieces of research on tomato are highly motivating to use silicon in *Solanum* crops as, unlike the other silicon-accumulating crops previously used for this type of research such as rice or maize, tomato is a silicon excluder crop [94]. Despite that, benefits under stress are still observed supporting the potential of silicon even in excluder crops.

Since the presence of drought stress can be hard to predict and to ensure plants can be protected at any point in their life, research has also focused on using biostimulants in a preventive way. In their study, Bindu et al. [95] inoculated tomato seeds before planting them and showed an enhancement of antioxidant enzyme activity under stress during their growth. This support the use of seed treatment, easier to implement on a farm, to increase plant tolerance.

A study by Vu et al. [96] highlighted that even if abscisic acid increased drought tolerance, various growth parameters were negatively impacted by the high-concentration treatments for well-watered plants. This observation is important to understand the limitations of biostimulants and the need for further research.

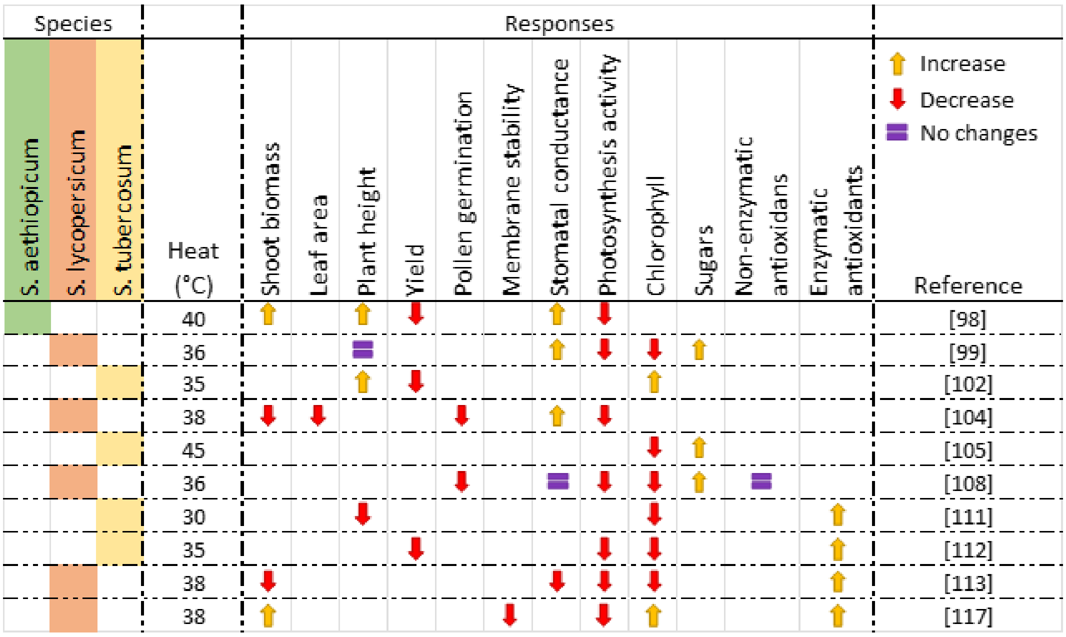
3.2 Heat

Elevated temperatures or extreme events such as heatwaves can hinder plant growth at every development stage depending on the cultivar, intensity and length of stress. In addition to morphological and physiological changes, antioxidant levels can also be affected by heat stress and increase a plant's nutritional value [97]. Short, measured stress can thus be beneficial, if timed right, for vegetable quality by improving 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

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

Table 2: A sub-sample of the available studies on the effect of heat on *Solanum* species. Each colour represents the *Solanum* species used in each study.



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	↑		↑	↓			↑	↓					[98]
	🟧		36			=				↑	↓	↓	↑			[99]
		🟨	35			↑	↓					↑				[102]
	🟧		38	↓	↓			↓		↑	↓					[104]
		🟨	45									↓	↑			[105]
	🟧		36					↓		=	↓	↓	↑	=		[108]
		🟨	30			↓						↓			↑	[111]
		🟨	35				↓				↓	↓			↑	[112]
	🟧		38	↓						↓	↓	↓			↑	[113]
	🟧		38	↑					↓		↓	↑			↑	[117]

↑ Increase
↓ Decrease
= No changes

[98]. Plant height and shoot weight, conversely, kept increasing under 40°C [98]. 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 [98]. This shows a different tolerance threshold for vegetative and reproductive growth which are important to uncover to understand the potential of the African eggplant in heat-prone fields.

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 [99]. When including more cultivars and setting the temperature at 40°C, Sherzod et al. [100] found an increase in plant height and stem diameter for many cultivars, especially the ones producing large fruits. Blanchard-Gros et al. [101] also found a cultivar-dependent response of plant height under heat when studying the wild tomato *S. chilense* with the increase in stem growth under heat for some. The same trend regarding plant height was noted in potato with an increase of 13°C from normal temperature leading to a plant height increase of 47% on average [102]. 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. [103] 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 suggests long-term damages and a slow recovery regarding vegetative growth.

Leaf production and development are, in general, hindered at high temperatures after a certain threshold as seen in both tolerant and sensitive tomato cultivars [104] and potato [105]. No change in leaf number was noted, however, in young tomato grown at 36°C and leaves produced were the same size in another study growing tomato at 40°C [99, 100]. 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.

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 [106]. In tomato, both short and long-lasting heat stress reduced pollen germination and the number of fruits produced [100, 107]. Pollen germination was decreased in both tolerant and sensitive cultivars even though the effects were most noticeable in the sensitive one [108]. 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 [108]. 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 [109].

Leaf pigments are also affected by heat with tolerant tomato cultivars displaying higher leaf pigment levels in a study by Zhou et al. [108]. Every potato cultivar investigated by Tang et al. [102] 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 [110]. A high number of light-harvesting proteins can be nefast for plants under heat as the stress limits the amount of light that can be used due to various damages. The excess light can eventually increase the damage to the photosynthesis apparatus and other processes. An increase in chlorophylls is, nonetheless, important to maintain and potentially enhance 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 [83]. 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 [111]. A range of studies supported that observation with a reduction in leaf pigments in potato [112], tomato [113], and the brinjal eggplant [114].

Tolerant tomato cultivars displayed an increase in stomatal conductance which was not observed in sensitive ones [108]. Both sensitive and tolerant tomato cultivars increased their stomatal conductance under heat in another study, however, suggesting a variation in the tolerance mechanisms [104]. This adaptive mechanism allows better leaf cooling and the maintenance of enzyme activity, crucial to maintaining photosynthesis. This was not observed by Zhou et al. [99] and Duan et al. [103] who reported a decrease in stomatal conductance, suggesting another way to limit the negative effects of increasing leaf temperature while maintaining water loss to a minimum. The photosynthesis apparatus is, in general, highly disturbed by heat through a range of mechanisms including enzyme denaturation and increased transpiration [97]. Photosynthetic parameters were reduced in tomato plants subjected to an increase of 15°C or higher [115, 116] but no negative effects were noted at a 6°C increase in another cultivar, showing a certain tolerance of the photosynthetic system [71]. Maximum photochemical efficiency of photosystem II (*Fv/Fm*) can be a powerful way of identifying heat tolerant plants as iys maintenance under heat stress is associated with multiple other tolerance traits [104, 108]. As a fast-responding indicator of a plant's photosynthesis efficiency, *Fv/Fm* can help researchers quickly identify damage to the photosynthesis process.

Oxidative stress, as measured by hydrogen peroxide (H_2O_2) concentration or lipid peroxidation, was induced by heat in tomato [116, 117]. 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 in a few studies [112, 113, 118]. Osmolytes are also often increased to maintain membrane stability and a range of cell processes, as was observed in a study by Dasgan et al. [118] 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 [105, 116]. A range of mechanisms is thus activated under stress to help maintain critical processes running.

3.2.3 Biostimulants to relieve heat stress

As the flowering stage is highly affected by heat, biostimulants improving pollen viability and flower survival are key to improving crop heat tolerance. *Ascophyllum nodosum* extract has often been used as an effective biostimulant and has shown a significant recovery in pollen viability in tomato under heat [119]. Eventually, fruit set and development can also be improved by the use of biostimulants under heat, ensuring income stability [120].

A range of other improvements can lead to high-temperature tolerance as seen in Niu et al. [121] where chlorophyll production and photosynthesis were recovered by the use of biostimulants, eventually leading to healthier plants. The increase in photosynthetic activity under stress was also reported by another study using different biostimulants, suggesting similar tolerance mechanisms induced in both cases [122]. Similarly to what was observed under drought, biostimulants also increase the antioxidant activity to mitigate ROS-mediated damage and improve heat tolerance, as seen in the study by Sang et al. [123] for example.

Biostimulants under heat have been shown to have a positive effect on tomato growth even at a seedling stage [124]. In contraction, only the final yield of the plants was improved in a study by Soares et al. [125]. Biostimulants can thus improve tolerance of only particular parameters at different growth stages, making it difficult to estimate their potential at an early stage. Only a few physiological and growth parameters were improved in a study by Francesca et al. [126] when biostimulants were used, supporting a variability in their use.

When comparing four tomato cultivars, Francesca et al. [127] reported large differences in the biostimulant effect. They seemed to have a positive impact mostly for the cultivars producing small fruits while fewer effects were reported for cultivars producing large fruits [127]. The differences noted in this paper may suggest that, depending on the inherent tolerance mechanism of the cultivar of interest, the biostimulant used may not lead to the same effects. These observations are important to understand the diversity of results from biostimulants, highly dependent on various conditions such as length of stress, concentration, or timing of application.

3.3 Salinity

Saline soils contain excessive soluble salts, mainly sodium chloride (NaCl) and sodium sulphate (Na_2SO_4). They are generally described as having an electrical conductivity higher than 4 dS/m [128]. This represented 412 million hectares of soil in 2015, 122.9 of which in Africa [128]. 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 [129]. 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 *Solanum* crops including morphological, physiological, and molecular pathways [130]. Table 4 depicts graphically some of the literature available on salinity effects on *Solanum* species.

3.3.1 *Solanum* species under salinity

Salinity stress affects *Solanum* species from the germination stage, with both tomato and its close relative the black nightshade *S. nigrum* displaying reduced seed germination under NaCl irrigation, even if *S. nigrum* was less affected [131]. Of the germinated seeds, both root and shoot growths were limited by the stress [131]. This negative effect on root and shoot was also observed in the plants' vegetative stages [132, 133]. Interestingly, even high levels of salt did not reduce plant

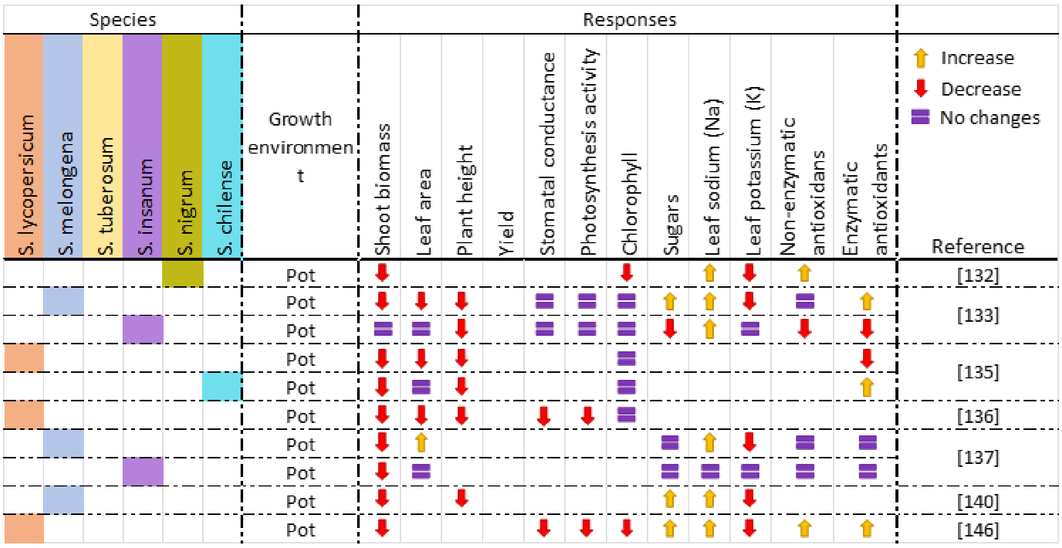
Table 3: Soil salinity classes in electrical conductivity EC_e

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

growth parameters in the wild eggplant *S. insanum*, highlighting the tolerance potential of some *Solanum* species [133]. *Solanum pennelli*, a salt-tolerant crop, formed the central focus of a study by Albaladejo et al. [134] in which the authors found a slow tolerance mechanism. Shoot and root growth rate was much slower in *S. pennelli* than in tomato after seven days of stress, but this was reversed after 14 days [134]. 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. Leaf development was reduced in the brinjal eggplant at lower salinity levels than stem or root development, showing differences between plant organs as well [133]. This decrease in leaf production was also observed in tomato [135], *S. chilense* [136], *S. nigrum* [132], and *S. insanum* [137]. The tolerant *S. pennelli* maintained leaf thickness under salt while the sensitive tomato displayed thinner leaves under stress [134]. 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. [133] reported the maintenance of LRWC in *S. insanum* up to 300 mM NaCl while the brinjal eggplant LRWC was reduced after 100 mM NaCl. A reduction in LRWC was also noted in two tomato cultivars [138], impacting leaf expansion, nutrient transfer, and photosynthesis

Table 4: Sub-sample of the available studies on the effect of salinity on *Solanum* species. Each colour represents the *Solanum* species used in each study.



Species							Responses												
S. lycopersicum	S. melongena	S. tuberosum	S. insanum	S. nigrum	S. chilense	Growth environment	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	↓						↓		↑	↓	↑		[132]
	■					Pot	↓	↓	↓		=	=	=	↑	↑	↓	=	↑	[133]
			■			Pot	=	=	↓		=	=	=	↓	↑	=	↓	↓	
■						Pot	↓	↓	↓				=					↓	[135]
					■	Pot	↓	=	↓				=					↑	
■						Pot	↓	↓	↓		↓	↓	=						[136]
	■					Pot	↓	↑						=	↑	↓	=	=	[137]
			■			Pot	↓	=						=	=	=	=	=	
	■					Pot	↓		↓					↑	↑	↓			[140]
■						Pot	↓				↓	↓	↓	↑	↑	↓	↑	↑	[146]

↑ Increase
↓ Decrease
= No changes

activity. A change in water status has also been observed regarding the leaf osmotic pressure in tomato, *S. chilense*, and potato which decreased under stress, enabling osmotic adjustments via the adapted osmotic gradient to limit ion accumulation as a short-term tolerance strategy [136, 139]. A reduction in leaf osmotic pressure was, however, only observed in the most sensitive brinjal eggplant accessions while tolerant ones maintain it under stress, suggesting other mechanisms in place for long-term tolerance [140]. 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. [141] and in the brinjal eggplant [142].

Variations in leaf morphology and water content can, in turn, affect chlorophyll levels. Under very high salinity levels (above 300 mM NaCl), chlorophyll was noticeably reduced in tomato plants [143]. A range of studies on *Solanum* reported no or little effects on total chlorophyll under more moderate salinity levels [133, 135, 137]. Carotenoids were, however, regularly reduced, suggesting a potential shift in light-harvesting wavelengths throughout the stress. Photosynthesis activity can eventually be affected due to a combination of affected pathways including light harvesting changes. Liao and Zhang [144] 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 tomato [135, 145], the brinjal eggplant and *S. nigrum* [133]. In addition, non-photochemical quenching, representing the amount of light dissipated as heat by the plant to avoid photodamage via the production of ROS, was increased in *Solanum* [146]. Despite this increase, ROS H_2O_2 and O_2^- were still recorded in high levels in these crops [146]. The increase of H_2O_2 is not consistent, however, with some reports of no effects of salinity [132, 137]. When comparing H_2O_2 levels in potato leaf, stem, and root, Jaarsma, Vries, and Boer [147] 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 and decrease of the potassium over sodium ratio in various plant parts. This disruption causes secondary negative effects including damage to the cell membrane and various enzymes. Albaladejo et al. [134] noted a clear sodium increase in roots and leaves of *S. pennellii* and tomato under salinity with *S. pennellii*, more tolerant than tomato, showing a less drastic leaf uptake. This clear increase was also noted in the brinjal eggplant and *S. insanum* alongside an increase in chloride ions [133, 142]. 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, necessary to ensure water flow through the plant [148]. Fruit sugars increased under salinity in the brinjal eggplant and tomato, but not in *S. chilense*, considered the most tolerant species among those [142, 149]. *S. insanum* accumulated proline and sugars to a higher level than the brinjal eggplant under stress [133]. 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 [148].

Changes in ROS level under salinity trigger an antioxidant response by crops, as observed by the increase of antioxidant enzymes in potato [139], tomato [146], the brinjal eggplant [142] and *S. nigrum* [144]. The antioxidant response can affect greatly crop tolerance as was seen in potato where the most tolerant cultivar showed an increase in shoot ascorbate peroxidase and glutathione reductase that was not observed in the sensitive accession [150]. Ahanger et al. [146] reported an increase in all antioxidant enzymes measured, total flavonoids and phenols in tomato, with the latter also increased in the brinjal eggplant fruits and tomato leaves in other studies [142, 145]. This antioxidant response seems to be triggered at low salinity levels as shown by Ben Abdallah et al. [132] 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 [132]. 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 [133, 151]. In some studies, no effects were noted at all [133, 149]. 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.

3.3.2 Biostimulants to relieve salinity stress

Similar to observations made for crops under drought or heat, some biostimulants have improved salinity tolerance in *Solanum*. Tomato plants grown under salinity reported an increase in leaf area [152], biomass production [153], and yield [154] when treated with biostimulants. The level of salinity has a noticeable impact on the effects of biostimulants, with very high salinity level hindering the biostimulant action, either due to the damage level induced in plants or to the direct inactivation of the active compounds [155].

The tolerance mechanisms of biostimulants can differ slightly, with a type of bacteria having no effect on chlorophyll levels but impacting mostly root development and proline accumulation [156]. The use of arbuscular mycorrhizal fungi (AMF), in opposition, did not impact root development but enhanced the root uptake of selected nutrients, limiting deficiencies [157]. Improving antioxidant response to reduce ROS damage was also a tolerance mechanism triggered by biostimulants [156].

Even if silicon has been associated with increased drought tolerance when used as a biostimulant, Costan et al. [158] showed that a positive effect was not seen under salinity. Indeed, despite a slight increase in fruit number under stress, the nutrient uptake and plant growth were not improved by silicon [158]. In cases like that, yield gains are too marginal to make the use of silicon viable for farmers due to the high cost not being covered by the limited benefits. The absence of a net positive effect was also seen when using flavonoids as biostimulants in salty conditions which improve leaf fluorescence but not overall photosynthesis or plant growth, limiting their overall benefits [159].

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 [160]. Heat and drought and a few other stress combinations on *Solanum* are discussed below.

3.4.1 Heat and drought

In a study by Francesca et al. [126], the growth of tomato 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. This was also observed by Duan et al. [103], suggesting that the positive effect of heat does not seem to compensate for the highly damaging effects of drought. This predominance effect is not always seen, however, with plant development reaching its lowest level under the stress combination in a range of studies [114, 161, 162]. The intensity and length of stress are major factors determining whether one stress will be predominant or not. 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 [101, 103]. When both heat and drought reduced chlorophyll levels individually, their combination seems to show an additive effect with a further reduction reported [114].

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 [101, 103, 126]. Overall photosynthesis was, however, generally further decreased by the stress combination [101, 114, 161]. 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 [116]. Under a less intense heat treatment reaching 32°C combined with no irrigation, plants mostly displayed characteristics of drought alone [71]. These results suggest a complex interaction of the stresses depending on their intensity and length which will determine the mechanisms of the plants to withstand stress.

H_2O_2 and MDA were further increased under stress combination, suggesting a stronger oxidative stress response [114, 161]. 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 [114, 161]. Hannachi et al. [114] reported stress hormones to be increased to the same levels as observed under drought alone while Francesca et al. [126] observed this in sugars. 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

Plant growth was only more affected by the combination of drought and salinity when salinity was present at a high level, following the same trend observed under heat and drought [163]. Before that level, 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 [163]. 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 [164]. This was further confirmed by leaf fluorescence measurements, supporting the importance of stress length and intensity when talking about tolerance and resistance [164]. A study in tomato plants by Ors et al. [165] 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 [166]. 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 limiting the negative effects of ion accumulation observed under salinity [167]. 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 [167]. This was further observed by Lopez-Delacalle et al. [168] 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. [169], 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 [169]. In another study, the highest decrease in photosynthetic activity was observed under the combination of stresses [170]. 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 and temperatures are high [171]. 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. [171] and antioxidants being regulated differently in the study of García-Martí et al. [170].

Thus, understanding field-like conditions is important to predict whether a stress interaction will be beneficial or detrimental based on each stress intensity.

3.4.4 The use of biostimulants in stress combination

Research on biostimulants in stress combination is limited on *Solanum* crops due to the relatively new interest in stress combination and biostimulants individually. Due to the unique and unpredictable effects stress combination can have on plants, biostimulants effective against one stress might not be effective when multiple stresses are present. Understanding how biostimulants react under the combination of stress is thus highly important. Despite suggestions that the combination of biostimulants is the most promising approach in field conditions [172], melatonin on its own has shown clear positive effects on tomato plants under simultaneous heat and salinity [173]. Plants under stress recovered their photosynthetic activity completely when melatonin was applied just before the stress occurred. Positive results were not seen in a study by Francesca et al. [126], however, when using a protein hydrolysate on plants under the combination of heat and drought, following the same pattern as its effect on each stress individually. The main component of the biostimulant used is thus highly important to ensure the benefits outweigh the cost. These results also show that, in some conditions, the observations made under individual stress can be extrapolated to the stress combination.

4 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. The African eggplant 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 its stress tolerance is sparse, however, despite some knowledge based on its evolutionary path. 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. Investigating its unique responses to a range of environmental stresses individually or in combination is key to helping fight food insecurity and crop diversity decline. In addition, quickly available solutions to increase field resilience against various environmental stresses are needed. Biostimulants are promising but their success depends on a variety of factors. 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.

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