Vol. 14(3), pp. 118-135, 17 January, 2019
DOI: 10.5897/AJAR2018.13668
Article Number: 3C65E4059891
ISSN: 1991-637X
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African Journal of Agricultural Research

Review

Crop abiotic stresses and nutrition of harvested food crops: A Review of impacts, interventions and their effectiveness

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Received 24 October, 2018; Accepted 3 December, 2018

In tandem with the accelerating effects of climate change, efforts to increase agricultural productivity to feed the growing population are still being extensively rolled out in Africa. That notwithstanding, a large population in the continent remains food and nutrition insecure; rendering malnutrition the biggest public health challenge. Coupled with the increased incidences of abiotic stresses, developing countries are particularly in dire need to seek options that will sustain both yield and nutritional value of their food crops. Presently, nutritional quality deserves more attention than yield alone, hence factors perturbing it are of an immense importance. While the effects of abiotic stresses on agricultural productivity are unequivocal, their influence on nutritional quality of food crops is still hazy. In the simplest presentation of the synergy between humans, plants and the environment; man gets nutrients from plants, which source nutrients from the soil (environment). We hypothesized that abiotic factors are a double-edged sword with unclear plausible consequences on nutritional status of food crops and consequently humans. In a multifaceted approach, this review concisely presents an overview of malnutrition in Africa, intimate synergy between agriculture and nutrition, and unravels the effects of abiotic stresses on the nutrition status of harvested crops. While the effects are dynamic under many factors, the present work uncovers that abiotic stresses predominantly increase antioxidants, proteins and carbohydrates due to their contributory role in abiotic stress tolerance. It further acknowledges the promising interventions that have been implemented in this light, but in order to impact significantly on human nutrition, we call for a more collaborative approach cognizant of the complexity of this phenomenon.

Key words: Abiotic stresses, nutrition, agriculture, antioxidants, climate change, breeding.

INTRODUCTION

The fact that climate is changing needs no formal introduction. Agriculture is faced with a double role as far

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as climate change is concerned; as a major contributor and as a major victim. The associated effects include increased incidences of abiotic (drought, salinity, heat, cold) and biotic (pests and diseases, invasive species) stresses and are expected to become even more prevalent in the future decades (Wang and Frei, 2011). Whether acting individually, or synergistically, these stresses cause fundamental reductions on growth and quality of crop plants (Ashmore et al., 2006), consequently putting a wretch on global food supply systems and nutrition of human population. Contrarily, demand for food has grown tremendously in the past decades, and is expected to further escalate as population reaches 9.7 billion in 2050 (United Nations, 2015) from the present 7.6 billion. Therefore, one of the largest problems the current and future generations are confronted with is the need to meet the food demands quantitatively and qualitatively.

This challenge has resulted into a flurry of research efforts by scientists, governments, non-governmental agencies and developmental partners (Lobell et al., 2008) aimed at maintaining agricultural productivity without perturbing the food supply for the current demand. As obviously expected, release of crop cultivars tolerant to different forms of stresses has dominated the efforts. Moreover, advancements in molecular technologies have added a remarkable value to this pursuit, enabling production of tolerant cultivars, biofortified food crops and high yielding crop cultivars. Meanwhile, breeding projects are underway aimed at adapting novel crop cultivars of key cereals to heat, drought and salinity (Pinto et al., 2010; Araus et al., 2008; Fleury et al., 2010; Ren et al., 2005). While commendable progress has been made with regards to adapting key crops to the changing environmental conditions, limited focus has been diverted on the nutritional quality. Recently, a number of studies have investigated the effects of different forms of abiotic stresses on nutritional quality of food crops. Mixed results have been revealed among and within crop species and abiotic stresses; hence no affirmative conclusion can be made regarding these effects. Considering the growing awareness for a more nutrition oriented production, commonly referred to as nutrition sensitive agriculture, efforts to improve nutrient status of key crop plants, in light of prevailing environmental factors are underway.

While these efforts, advances and achievements are conspicuous and commendable, the question arises as to whether these have had a significant impact on nutrition. Moreover, what is agriculture for? Primarily, it is in our firm belief that agricultural interventions, must chiefly aim at improving nutrition status of crops, hence people. Cognizant that crop agriculture and human nutrition are intimate and inseparable, interventions to improve agriculture must be carefully regulated so as to balance with human nutritional needs. Presently, less effort has been made to study and elucidate the impact of abiotic stresses on quality of harvested crops.

In a nutshell, environmental factors elicited by climate change have led to a myriad of abiotic stresses, such as changes in precipitation (high rainfall, low rainfall, truncated or prolonged rainy seasons), accumulation of salts in soils (salinity), temperature extremities (heat shocks and chilling), elevated carbon dioxide (eCO_2) and depletion of the ozone layer among others (Figure 1). These have varying effects on crop production, and their immediate effects *in situ* (on the field) include reductions in growth, activation, up and down-regulation of some stress responsive biochemical and physiological processes and how a crop responds to each stress varies. Initiated *on situ* but significantly impacting *ex situ* are the changes in yield and nutritional quality, which again, depend on the crop species, development stage of exposure to the stress, duration and severity of stress, etc.

This review, presents an outlook on different view points and perspectives, of how different abiotic stresses affect agricultural productivity, with particular focus on nutritional composition; briefly analyses key roles of the affected crop food nutrients in humans; and the interventions that have been made aimed at maintaining productivity and nutritional status of food crops and how effective they have been. It further highlights missed opportunities and gaps and proposes plausible interventions.

Overview of malnutrition in the African region

In developing countries, the battle against malnutrition is far from won. Currently, under nutrition co-exists with over nutrition in Africa and even globally (FAO, 2017). Meanwhile, efforts in fighting hunger have seen an overall improvement in combating under nutrition, but increased urbanization, lifestyle changes, and other resource pressures have resulted in poor diversity in the food baskets available and consumed, thus an increment in over nutrition and micronutrient deficiencies. The focus of programmes and interventions have shifted from only tackling under nutrition to a more combined approach of fighting against what is known as ‘triple burden’ of malnutrition in Africa (FAO, 2017; De Valenca et al., 2017)

Malnutrition simply means ‘bad nutrition’ and it is used to describe a person in a state in which the physical function dwindles to an extent of inadequate capacity to maintain sufficient bodily performance processes such as growth, pregnancy, lactation, physical work and resisting and recovering from diseases and infection (Bain et al., 2013). The problem of micronutrient deficiency draws the need for action, just as under nutrition and over nutrition in Africa as it bears grave consequences to overall health. Food quality and nutrient density in foods is a result of a number of factors (both biotic and abiotic factors). Crops gain nutrients from the soil, and humans

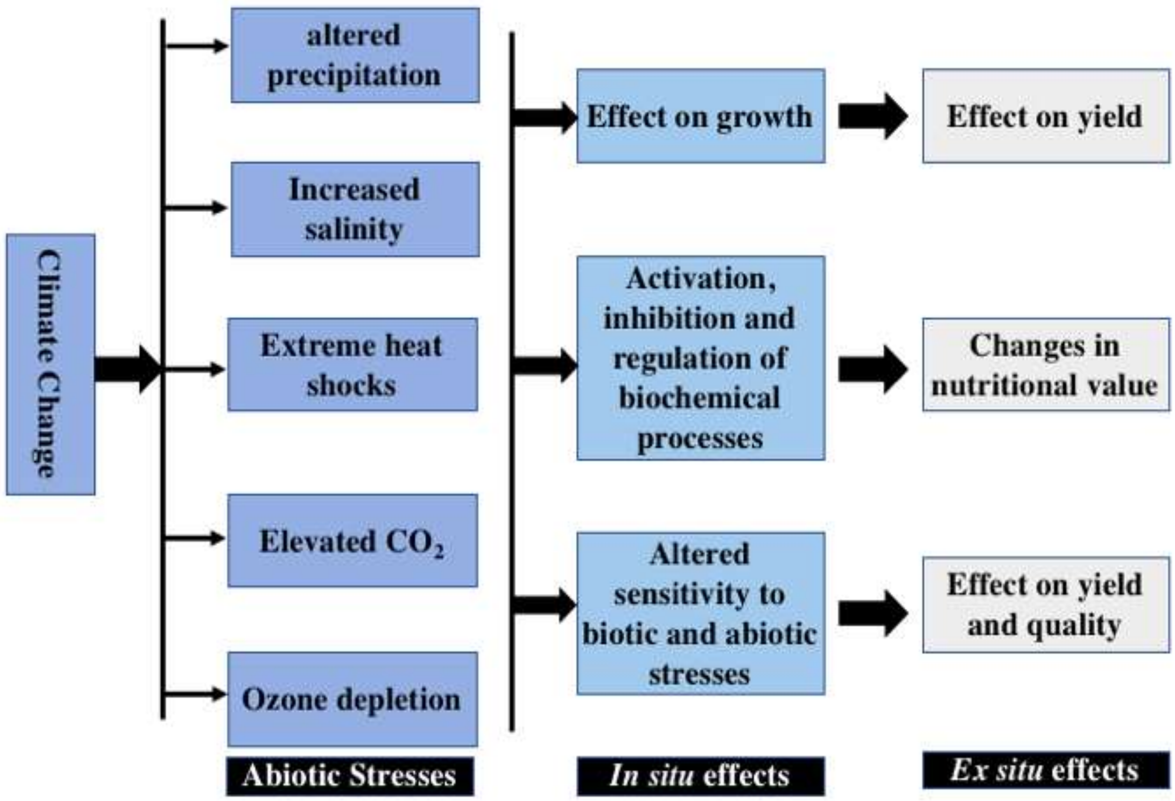

Figure 1. Schematic illustration of how environmental changes brought by changes in climate impacts on agricultural production and ultimately on nutritional quality and yield. Current observable consequences of climate change have altered rainfall patterns and quantities (droughts and flooding), induced accumulation of osmotically active salts in the soil, extremes in temperatures (heat shocks and chilling), high CO_2 levels etc. Depending on their severity, these may cause some forms of abiotic stress to crop production, whose direct effects on site may be changes in growth and ultimately yield. Physiologically, various biochemical processes will be induced, altered or inhibited, in response to these. Ultimately, these have a prominent bearing on the final nutrient content of harvestable food products.

and animals, in the simplest model, consume nutrients from such crops (Grusak and DellaPenna, 1999). Therefore, when considering the fight against both food and human nutrition issues (of public health concern), it is relevant to consider how integrated interventions can be put in place to tackle the factors that correspondingly affect the environmental resources for food availability and quality (nutrient density).

The relationship that exists between the three forms of malnutrition and their effects, gives a picture for the need of a more synergistic approach, and increased investment in malnutrition. Figure 2 shows the link that exists between under nutrition, over nutrition and micronutrient deficiencies. Considering that humans and animals get nutrients from plants, whose primary source is the soil, factors that constrain uptake, transportation, mobilization and utilization of these nutrients from the soil to the plant are of immense significance.

Under nutrition is a form of malnutrition expressed by wasting (having low weight for height), stunting (being too short for current age) and underweight. These are the anthropometric indices for the assessment of a child's nutritional status, considering that much emphasis skews towards children under the age of five in under nutrition related discussions. According to the United Nations Children Fund in 2017, nearly 50% of all deaths in children below the age of 5 were attributable to under nutrition, and this meant 'a loss of about 3 million lives of children'. The picture of stunting as a form of under nutrition is daunting in the African region, especially the sub-Saharan Africa (SSA) region, than any other region. About 38% of children in the African region were stunted and over 6% of children were wasted and there has been an increase in the absolute number of stunted children from 52 to 60 million in the period between 2000-2015 (WHO, Monitoring health for the SDGs: sustainable development goals. Geneva (2016). The Millennium Development Goals report (2015) reported that in sub-Saharan Africa, 39% of children under 5 years of age were stunted, 10% were wasted while 25% were underweight.

Children who are undernourished have an increased

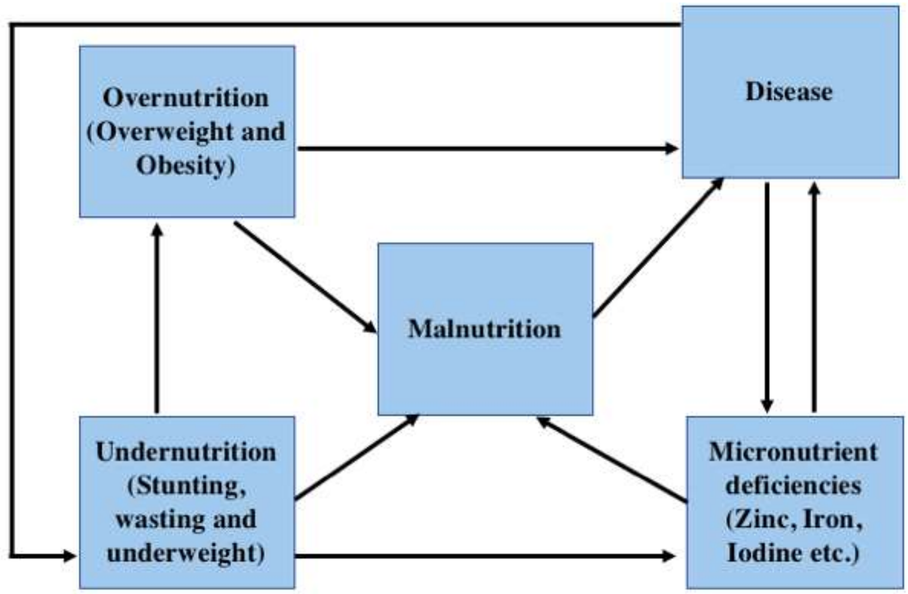

Figure 2. Link between the three forms of malnutrition: In the simplest presentation, undernutrition, overnutrition and micronutrient deficiencies are all forms of malnutrition, i.e. 'bad' nutrition. Undernutrition may result in micronutrient deficiencies as the body's nutrient metabolism and absorption is altered, and this can in turn result in different diseases such as Iron deficiency Anaemia (IDA) and other micronutrient deficiency disorders. Diseases such as diarrhoea can also result into micronutrient deficiencies since they alter integrity of the small intestines in nutrient absorption. Undernutrition in early childhood increases the risk of being overweight or obese later in life. Overnutrition is a risk factor for different chronic diseases such as diabetes mellitus and Cardiovascular Diseases (CVDs). Presence of disease as a result of one form of malnutrition can result into development of another form of malnutrition. For example, micronutrient deficiencies can result into disease which could in turn result into undernutrition.

risk of dying before reaching adulthood, and have poor physical and cognitive development (Jones et al., 2014). A recent meta-analysis of child malnutrition distribution in Africa using the Demographic and Health Survey (DHS) data from 32 countries found that stunting was highest in East Africa (57.7% in Burundi), and lowest in Central Africa (39.9% in Chad) (Akombi et al., 2017). Wasting was highest in Niger (18.0%) and underweight was highest in Burundi (28.8%) and Chad (28.8%) (Akombi et al., 2017). All these figures are unacceptably high, and give an overview on why under nutrition is of public health concern in SSA. Diverse factors predispose children to under nutrition. Some of the commonly reported risk factors include low mother's education, low socio-economic status, poor dietary diversity, sex of child (with male child at increased risk), low birth weight, underweight mothers, poor sanitation and hygiene, just to mention a few (Akombi et al., 2017; Akombi et al., 2017; Parkes et al., 2017). Understanding such risk factors is important in formulating interventions that target the modifiable risk factors, and thus help in combating under nutrition.

Another form of malnutrition is over nutrition. An individual is said to be overweight or obese when the Body Mass Index (BMI) is 25.0 to 29.9 kg/ m^2 and ≥30.0 kg/m^2,respectively (WHO, Waist circumference and waist-hip ratio: report of a WHO expert consultation, Geneva, 8-11 December 2008., 2011); BMI remains one of the recommended methods of assessing nutritional status of populations, especially in adults. Globally, the 21st century has been met with an increase in overweight and obesity not only in vulnerable groups such as children and women of reproductive age, but also in men. The focus is on women in the pre-pregnant phase and the reproductive age, as they form the focal point of the continuous cycle of overweight and obesity in the children to be born. In the African region, the epidemiological transition and nutrition transition has resulted in triple burden of malnutrition; micronutrient deficiencies, over nutrition and under nutrition; hence overweight and obesity have equally become significant problems of public health concern (WHO, 2011).

A recent secondary analysis of Demographic and Health Survey data for the period from 1991-2014 in 24 African countries showed an increase in prevalence of overweight and obesity in all the 24 countries in urban women aged 15 to 49 years (Amugsi et al., 2017). The trend calls for greater attention to this issue. For example, within the period of 1991-2014, obesity in women of this age group doubled in countries like Kenya, Niger, Rwanda and Ivory coast, among others and tripled in others like Malawi, Zambia, Tanzania, Ethiopia, among other countries (Amugsi et al., 2017). A number of studies have also reported a high increase in the prevalence of overweight and obesity in young children and adolescents in different African nations (Negash et al., 2017; Ajayi et al., 2016). In South Africa, persistent low social economic status, physical inactivity, heavy alcohol use and tobacco consumption were some of the rampant risk factors (NCD Risk Factor Collaboration (NCD-RisC)–Africa Working Group, 2017). In addition, increased intake of poor diets and 'fast foods', which are characterised by more fats and less fibre, are also a significant cause of overweight and obesity and increased risk for non-communicable diseases in Africa (Welch and Graham, 2004).

As previously mentioned, malnutrition can also be presented as an imbalance or inadequate availability of micronutrients in the body; this is known as micronutrient deficiency or hidden hunger. Globally, over 2 billion people have 'hidden hunger' (Herrador et al., 2014). Particularly, African countries have exacerbated cases of micronutrient deficiencies. Micronutrient deficiencies are due to inadequate dietary intake, increased losses from the body, and/or increased requirement; and mostly affect children and pregnant women, and many other population age groups (Herrador et al., 2014). Micronutrients of known public health importance include the following: zinc, iodine, iron, selenium, copper, vitamins A, E, C, D, B2, B6, B12 and folate (Herrador et al., 2014). A study on global trends in dietary micronutrient supplies and dietary intake found that although most regions such as South East Asia have seen a decline in the prevalence of micronutrient deficiencies and increment in food micronutrient density, sub-Saharan African region has seen a decline in the micronutrient density in its food system (Beal et al., 2017). In sub-Saharan Africa, the problem is a particularly major issue, because 28 in 100 people in 2011 were consuming a diet inadequate in essential micronutrients (Beal et al., 2017). A systematic review of micronutrient status in women of reproductive age and pregnant women in African countries (that is Ethiopia, Kenya, Nigeria and South Africa) found that iron deficiency prevalence ranged from 9 to 16% in these countries, and Iron Deficiency anaemia was at 10% (Harika et al., 2017). Further, Vitamin A, zinc, and iodine deficiencies were equally more prevalent in the two age groups, indicating the magnitude of micronutrient deficiencies and inadequate intake (Harika et al., 2017).

The intimate synergy between agriculture and nutrition

Hawkes and Ruel (Hawkes and Ruel, 2008) assert that there is a direct relationship between agriculture (food production) and food consumption, narrating that increases in food production translate into increased food availability. However, relationship between agriculture and human nutrition is multi-step and sensitive to nuisance factors, hence far more complex to establish. An argument that the primary goal of agriculture is to improve the nutritional status of the population has been put forth (Haddad, 2013). While about 5 decades ago, agriculture was predominantly considered an economic activity due tothe rising population that was consequently followed with food shortages; the focus has recently changed, aiming at maximizing agricultural nutritional potential (Hawkes and Ruel, 2006). In a gradual learning process, the attention has registered to a shift from staple food production to more micronutrient rich foods, addressing key issues of hidden hunger. Moreover, in developing countries, limited and subsistence investments in the agricultural sector imply that most agricultural produce are primarily used for food on a household, communal and national level. Thus, a number of pathways are currently known, describing the synergy between agriculture and nutrition (Yosef et al., 2015; Kadiyala et al., 2014). Yosef et al. (2015), in their study reviewing 60 articles summarized a total of 6 pathways, while Haddad et al. (2013) summarized only 5, yet more or less identical to Yosef et al. (2015) (Table 1).

The major pathway describes *Agriculture as a Source of food* in which farmers primarily produce agricultural produce to supply their households with daily food requirements. From the produce, farmers ought to obtain calories, macro and micronutrients vital for human development. It is logical to assume that households that cultivate and produce more highly-nutritious foods are likely to use a proportion of it for their own consumption (Haddad, 2013). Such households tend to be heathier. For example, production of fruits and vegetables and their consumption will invariably increase intake of essential micronutrients such as zinc, iron, Vitamin A, calcium, etc. (World Bank, 2007) under conditions that intra-household food distribution is favorable. However, increased production should be more qualitatively focused than quantitative. For an instance, during the green revolution, most governments in Africa placed emphasis on increased production of staples, such as maize, wheat, rice, etc.; consequently, reducing price of food considerably. Notwithstanding such increases in yield, production gains did not translate into nutritional gains, inasmuch as most staples lack essential micronutrients required for children, pregnant women and the sick (Hawkes and Ruel, 2006). Moreover, households could hardly access and afford the increased food supply, hence increased agricultural production for food must be geared at addressing both nutritional quality and accessibility to bear the much needed impact.

Another key pathway links agriculture with nutrition as *an Income-Oriented production,* which produces surplus for sale. The market-oriented agriculture becomes more

Table 1. Pathways through which agriculture relates with and contributes to nutrition.

No	Pathway	Description	References
1	Agriculture as a source of Food	Production of nutritious food for household consumption	Haddad (2013); Kadiyala, et al. (2014); World bank (2007); Hawkes and Ruel (2006)
2	Agriculture as a source of Income for Food and NonFood expenditures	Proceeds derived from selling of surplus food harvests as funds for purchase of other food and non-food products	(Hawkes and Ruel (2006); Haddad (2013); Hawkes and Ruel, 2008)
3	Agriculture policy & Food prices affecting food production	Sufficient and surplus food production lowers food prices	Yosef et al. (2015); Haddad (2013); Hawkes and Ruel (2008); Torlesse et al. (2003)
4	Women in Agriculture & Intrahousehold Decision Making and Resource Alloccation	Women active in agricultural programs make sound household nutritional related decisions.	Hawkes and Ruel (2006) Yosef et al. (2015); Hawkes and Ruel (2008)
5	Female employment		
6	Women in Agriculture & Maternal Nutrition and Health Status and agriculture Associated Health Hazards		

important than subsistence Agriculture, as it provides income beyond domestic food needs, such as education and health, which ultimately have a bearing on nutrition (Yosef et al., 2015). Marketing issues such as tradability, demand and supply, comparative advantage and prices inform households' decisions on crop choices (World Bank, 2007). However, it is also not straightforward, that incomes generated from agricultural livelihoods would be used to improve nutrition, whether implicitly or explicitly. Hence, intra-household factors such as education, knowledge, decision making power income control and access to use of health and sanitation services determine the subsequent translation of increased production into improved nutrition (World Bank, 2007; Berti et al., 2004).

Women in Agriculture and Intra household decision making and resource allocation

This comes into play, cognizant of the special role women play on household nutrition, particularly among children. Studies have indicated that women who take part in horticultural programs have better nutritional outcomes. Consequently, deliberate efforts have been implemented to encourage women's participation in agricultural development strategies. For instance, households whose women participated in a gardening program produced and consumed 1.9 and 1.2 fold more fruits and vegetables, respectively, than their controls (Bushamuka et al., 2005). Furthermore, women subjected to nutritional education have better decision-making capacity with regards to distribution of agricultural produce for household consumption. As a consequence, such households increased target consumption tremendously, hence reducing Vitamin A deficiency (VAD) (Marsh, 1998). In a related scenario in Kenya, supporting women in production of orange fleshed sweet potatoes increased both consumption and nutritional outcomes when co-implemented with appropriate strategies that encourage correct child feeding and care practices (Hawkes and Ruel, 2006).

Agricultural policy and food prices unequivocally affect food production

This pathway assumes that increasing food production adjusts prices downwards and vice versa. Reduced prices result into an affordable access to nutritious food. More nutritionally rich benefits will be derived if decreases in prices are in nutritionally rich food crops such as fruits and vegetables. It is hypothesized that macroeconomic food policies that keep food prices low are likely to impact positively on nutrition (Torlesse et al., 2003). Moreover, it is substantiated, that volatility in food prices affect calorie intake. However, self-sufficient households are more resilient to such effects (Verma and Hertel, 2009).

Other pathways described by various authors include *Female employment in Agriculture and Child Care and Feeding; Women in Agriculture and Maternal Nutrition and Health status and Agriculture-Associated Health hazards* (Yosef et al., 2015) both of which recognize the unique role women play in agriculture. Taken together, all these demonstrate an inseparable synergy between agriculture and nutrition, whether explicitly and implicitly. Therefore, in order to attain required nutritional goals in Africa, interventions made in the agricultural sector must carefully consider nutritional status of the final crop produced. It must remain considered, that if nutrition is the final impact to be achieved, then agriculture must be the starting point.

Implications of abiotic stresses on agricultural productivity and nutritional value of food crops

As a result of climate change, there are various abiotic affects that are associated with it (Figure 1), with a considerable bearing on agriculture. When plants are exposed to an environmental stress, various physiological processes are altered, perturbed (Kamanga et al., 2018) and elicited, which may affect chemical composition; consequently, affecting the nutritional status of a harvested product (Wang and Frei, 2011). For example, drought stress reduces the photosynthetic capacity and cation uptake and translocation of tomato plants (Kamanga, Unpublished), which may limit carbohydrate synthesis. However, responses to environmental stresses are very complex, considering the multigenic nature of stress tolerance traits. In order to obtain a full picture, it is imperative to investigate interactions between plant structure, function and environment at the species, cellular and molecular levels (Barnabás et al., 2008). It is believed, that even slightest improvements in stress tolerance would improve yield and quality of crop plants in developing countries (Hoisington et al., 1999). Cognizant of the current prevailing malnutrition levels in developing countries, plant agriculture needs to be tightly monitored and regulated, considering that it is the most affordable and available nutrient source for a majority of households with limited access to animal food products and other forms of dietary supplements. Such communities are vulnerable in circumstances where abiotic stresses negatively affect agricultural productivity and nutrition. Hence, the need for a better understanding of such influences on both productivity and nutritional quality is worthwhile as it will ably inform relevant stakeholders in designing and delivering suitable interventions.

Effects of abiotic stresses on protein content and amino acid accumulation

Both humans and animals rely on crop plants for a protein source. Despite the relatively smaller amounts of protein in crops (10 to 30% DW), plant protein foods contribute approximately 65% of per capita supply of protein worldwide (Young and Pellett, 1994), and many studies have confirmed their prime role in reducing cardiovascular diseases (Richter et al., 2015). Nutritional importance of some crops, particularly cereals, is primarily determined by their protein content.

How sensitive protein content is to abiotic stress in a crop plant, depends on its genotype, severity and duration of the stress. Generally, most crop species have responded to adverse environmental conditions with increases in protein content (Table 2). These responses are non-uniform, varying in crop species, cultivars and genotypes, some showing decreases and some registering no effect. Good et al. (1994) found a linear increase in amino acid content with advancement of drought stress in *Brassica napus* (Oil /rapeseed). However, overall reductions in protein synthesis were registered as drought progressed, with resumptions in synthesis after re-watering. Contrarily, in another study (Triboi and Triboi-Blondel, 2002), heat stress was found to increase protein concentration in the same species. Subjecting oilseed to doses of ozone significantly reduced per seed content of protein. However, at harvest, protein content increased, which was primarily ascribed to the compensation from increase in seed size as the crop progresses (Bosac et al., 1998). Yet, another study investigating the effect of ozone on protein of oilseed did not find any significant differences (Ollerenshaw et al., 1999). Such intraspecies and intra-stress differences may point to the importance of timing, duration of stress and crop development stage.

Amino acid, such as proline (Kamanga et al., 2018), content of plant products has also been widely studied under abiotic stresses. Many studies have obtained significant increases in proline content under water stress. Presently, researchers have correlated these increases with tolerance to abiotic stresses such as drought, heat and salinity. Despite the controversy brought forth by this assertion, proline accumulation in tolerant cultivars aids in osmotic adjustment that enables maintenance of turgidity. As a consequence, some transgenic plants having higher proline expression under abiotic stresses have been produced in non-food crops such as tobacco, and have exhibited higher tolerance to abiotic stress. In a study by Abid et al. (2018) in wheat, the concentration of soluble protein was severely reduced, while that of free amino acids and proline increased significantly, under drought conditions. Conversely, a greater increase in amino acids and proline was observed under drought, with the decreases being more pronounced underSevere stress than Moderate stress. Cultivar sensitivity also seemed to influence the response, with sensitive cultivars showing a lower magnitude of increase in amino acid and proline concentration and a higher reduction in soluble protein than the tolerant cultivar. Presently, proline is acknowledged as the main component of osmotic adjustment, in addition to its prime role in aiding ROS scavenging and stabilization of cell membranes (Matysik et al., 2002; Kamanga et al., 2018). In wheat grains and Soybean seeds, protein content increased as a result of induction of both drought and heat. In a study by Ozturk et al. (2004), continuous water stress in wheat increased grain protein content by nearly one fifth (Ozturk and Aydin, 2004). Water stress has been found to increase protein content in barley

Table 2. Effects of various crop abiotic stress factors on proteins/ Amino acids.Either all species with author name, or all without, these all not in italics. Remarkably all spp. are named by Linnaeus.

Stress	Crop species	Effect ↑	Effect ↓	Effect —	Previous studies
Drought	*Brassica napus* L. (Oil seed)	√	√		Good and Zaplachinski (1994)
	Hordeumvulgare L. (Barley)	√			Savin and Nicolas (1996)
	Zea mays L. (Corn)	√			Oktem (2008)
	Arachis hypogeal L. (Peanut)	√		√	Dwivedi et al. (1996)
	Solanum tuberosum L. (Potato)	√			Teixeira and Pereira (2007)
	Triticumaestivum L. (Wheat)	√			Ozturk and Aydin (2004)
Heat	*Brassica napus L*. (Oil seed)	√			Triboi and Triboi-Blondel (2002)
		√	√		Abid et al. (2018)
	Helianthus annuus L. (Sunflower)	√			Triboi and Triboi-Blondel (2002)
	Triticum aestivum L. (Wheat)	√			DuPont and Altenbach (2003)
	Oryza sativa L. (Rice)	√	√		Lin et al. (2010)
Salinity	*Solanum tuberosum* L. (Potato)	√			Teixeira and Pereira (2007)
Ozone	*Brassica napus* (Oil seed)		√	√	Bosac et al. (1999)

(↑) abiotic stress increased protein / amino acid concentration: (↓) abiotic stress decreased protein / amino acid concentration; (—) abiotic stress did not cause any significant effect on protein / amino acid concentration.

(Savin and Nicolas, 1996), corn (Oktem, 2008), Peanut (Dwivedi, et al., 1996), Potato (Teixeira and Pereira, 2007) and Soybean. Wheat is by far the most extensively studied crop species in this regard. For a more comprehensive review (Wang and Frei, 2011).

Effect of abiotic stress on mineral content of food crops

Mineral nutrition remains among the crucial determinants of growth both in humans and plants. In plants, it is generally accepted that increased supply of crops with mineral nutrients results into increased yield and quality. As a consequence, various studies have been conducted to assess the net effect of reduced nutrient supply, through reduced fertilizer application or planting in growth medium devoid of the mineral nutrients of interest. Overall, the results have corroborated their prime role on growth, yield and quality (Taiz and Zeiger, 2010). However, a few studies have attempted to investigate the interactions between non-mineral abiotic stress such as drought, salinity, elevated carbon dioxide concentration etc, on the mineral nutrient status in edible plant organs. Presently, it is known, that water stress reduces bioavailability of nutrients in the soil and their transport to the plant organs (Oktem, 2008). However, notwithstanding the reduced uptake and bioavailability, some studies have established that severe drought stress increases concentrations of some macronutrients such as calcium and magnesium, and some micronutrients such as copper and zinc in grains of corn (Da Ge et al., 2010). The justification for the increase was related to the improved routes and transport mechanisms for the cations. In our study, investigating the physiological responses of two tomato cultivars with contrasting tolerance, to water deficit stress (Kamanga, Unpublished) however, found decreases in calcium and magnesium in non-food organs of tomato (stems and leaves), with increases in roots.

However, tomato fruits, while not assessed for their macronutrient levels, showed severe calcium deficiencies, with water soaked tissues involving cell breakdown followed by loss of turgor as described by Simon (1978). However, in another study by our group (Kamanga et al. 2018) we found increases in both calcium and magnesium in leaf tissues of tomatoes. In grains, decreases in P and K were found in corn subjected to lower moisture content (Da Ge et al., 2010), which was ascribed to their reduced bioavailability.

In addition to soil water stress, soil salinity has also been extensively studied and its relations with mineral nutrition have been elaborated (Grattan and Grieve, 1998). Overall, salinity affects crop performance and food nutritional quality, via altered nutrient availability, competitive uptake, transport and organellar partitioning of mineral nutrients within the plants. Grattan (1998) asserts that high concentrations of Na and Cl in the soil solution depresses nutrient-ion activities, leading to extreme Na/Ca, Na/K, Ca/Mg, and Cl/NO_3^- ratios. This increases plant's susceptibility to osmotic and specific-ion injury as well as to nutritional disorders that may result in reduced yield or quality.Potassium is amongst key minerals affected by salinity, inasmuch as high levels of external Na interferes with K acquisition by roots, disrupts root membrane integrity and alters their selectivity (Grattan and Grieve, 1998). Studies by various researchers (Kamanga, Unpublished; Izzo et al., 1993), have shown K decreases when Na is increased, which has been implicated in growth and yield reductions in tomatoes, spinach and maize (Song and Fujiyama, 1996; Chow et al., 1990; Botella et al., 1997).The decreases in K concentration in plants subjected to higher salinity are as a result of the competition between K and Na ions, which results into lower K:Na ratios (Kamanga, Unpublished) due to excessive uptake of Na and reduced K absorption. It is reasonable, therefore, to suggest that plants that maintain a higher shoot K:Na ratio under high salinity exhibit a key tolerance mechanism, principally relying on exclusion of sodium ions from the shoots by accumulating them in the roots, and in some cases compartmentalizing them in the vacuole separate from the cytosol (Greenway and Munns, 1980).

Salinity affects ion balance of various other mineral elements in the soil, consequently their concentration in plant tissues and organs. Calcium is amongst those that have been recorded. Presently, it is known that Ca availability is sensitive to Ca supply in the soil, nature of counter ions, pH and ratio of Ca to other cations (Grattan and Grieve, 1998). Fruits are particularly sensitive to Ca deficiencies owing to the differences in transport mechanism in various plant organs (Simon, 1978). Moreover, leaves, fruits and meristematic regions act as competitive sinks for Ca, exerting an influence on its preferential distribution (Clarkson, 1984). In plants whose marketable produce is primarily a leaf enveloped head, such as cabbage and lettuce, calcium is diverted from meristematic tissues due to excessive transpiration by outer leaves (Bangerth, 1979). Increased salinity elevated the incidence and severity calcium deficiency of artichoke buds, resulting into necrosis and one fifth reduction in marketable yield (Francois et al., 1991; Francois, Salinity effects on bud yield and vegetative growth of artichoke (*Cynara scolymus* L.), 1995). In cabbages, calcium deficiencies have also been observed in salt-stressed Chinese cabbage (Osawa, 1962). In general, salinity reduces Ca availability, transport and mobility to growing plant regions resulting into reduced quality of both vegetative and reproductive organs (Grattan and Grieve, 1998). Other forms of abiotic stress, such as ozone, narrowly affected macronutrient concentration (K, P and Mg) in corn; however, it increased Zn, iron and copper (Garcia, et al., 1983). A similar study conducted with potatoes produced contrasting results, showing increases in K and Mg, while Ca remained unaffected (Piikki et al., 2007). This was ascribed to a reduction in biomass accumulation relative to macronutrient intake. In carrots, subjecting plants to drought stress at the 4-6 leaf stage reduced Mg concentration, when grown on a course sandy soil. In the same study, when drought was imposed prior to harvest, an increase in dry matter was associated with a decrease in potassium and nitrate (Sørensen et al., 1997).

Effects of abiotic stresses on antioxidants

The current flurry of research relating to abiotic stresses has resulted into an elucidation of a myriad of physiological responses elicited by abiotic stresses. Key to the fate of these stresses, is the accumulation of antioxidants. A large amount of evidence reveals that under abiotic stresses, reactive oxygen species (ROS) production increases, which consequently results in cell death, lipid peroxidation and damage of the photosynthetic machinery (Kamanga et al., 2018). In order to scavenge such ROS, plants have evolved multiple mechanisms, including production of antioxidants; both enzymatic and non-enzymatic. While a significant amount of data is available on antioxidants accumulation under abiotic stresses, limited studies have made an effort to study the effect of such abiotic stresses on antioxidant levels in edible crop parts. In human diets, antioxidants are also a major determinant of nutritional quality of food. Fruits and vegetables are by far among key suppliers of antioxidants in human diets. In general, subjecting plants to abiotic stress invariably increases antioxidant concentrations. In a comprehensive review by Wang et al. (Wang and Frei, 2011), about two thirds of studies reviewed reported increases in concentration of phenolic compounds, one-tenth showed decreases while the remainder did not indicate any clear differences. Studies have established, that phenylpropanoid, a key enzyme in the biosynthesis of phenolics is stimulated by exposure to abiotic stresses (Oh et al., 2009; Kangasjarvi et al., 1994; Guo et al., 2008). As such, significant increases in phenolic compounds have been found in potatoes (Andre et al., 2008), grapes (Deluc et al., 2009), and rapeseed (Bouchereau et al., 1996) under drought stress; likewise, broccoli (Lopez-Berenguer, et al., 2009), raspberry (Neocleous and Vasilakakis, 2008) and strawberry (Keutgen and Pawelzik, 2007) under salinity stress, and in other crop species such as apples, grapes, lettuce, spinach and tomato (Wang and Frei, 2011).

Apart from phenolics, ascorbate (AsA), also known as Vitamin C, is also among the key antioxidants produced by plants under abiotic stress (Sharma et al., 2012). Ascorbate is a considerably abundant, yet less studied low molecular weight antioxidant and has demonstrated a key role in defense against oxidative stress caused by enhanced levels of ROS. Under abiotic stress, ascorbate is particularly useful, enabling scavenging of ROS, by reacting with superoxide radicals and hydrogen peroxide (Noctor and Foyer, 1998). Tomatoes, one of the notable suppliers of Vitamin C (ascorbate), have invariably shown increases in ascorbate content when subjected to drought stress (Zushi and Matsuzoe, 1998; Veit-Köhler et al., 1999; Favati et al., 2009). In plants, a majority of the

AsA pool results from a precursor (D-mannoseandL-galactose), dubbed the Smirnoff-Wheeler pathway, which proceeds via GDP-D-mannose, GDP-galactose, L-galactose, and L-galactono-1,4-lactone (Wheeler et al., 1998), a process not found in most animals and humans. Therefore, synthesis of these precursors de novo influences the ascorbic level in plants, required in human diets. As such, differential capacities to synthesize the necessary precursors result into differences in the plant's response under abiotic stress.

For example, in a study by Sorenson et al. (Sørensen et al., 1997), subjecting carrots to severe drought stress increased both Vitamin A (carotenes) and Vitamin C (AsA). When drought was imposed at specific growth stages, no significant changes were observed. Contrarily, reductions in carotenoid contents were observed in wheat subjected to severe and moderate water stress, with the reductions being more pronounced in sensitive cultivars (Abid, et al., 2018). Carotenoids are known to be involved in the dissipation of excess energy absorbed by photosynthetic pigments, which prevents formation of superoxide anions, an ROS, in plants receiving too much more energy than it can potentially utilize due to reduced photosynthesis (Reddy et al., 2004).Thus, maintenance of higher carotenoids in tolerant, relative to sensitive, cultivars may have enhanced photo-protection of the plant's photosynthetic apparatus. Reduced glutathione (GSH) is among the studied antioxidants produced in plants. In a study by Abid et al. (2018), both moderate and severe drought conditions increased the accumulation of GSH with the accumulation being higher in sensitive than tolerant cultivars. However, as drought period progressed, accumulation of GSH decreased. Similar results were also obtained in wheat by Herbinger et al. (2002). GSH plays an antioxidant role by directly scavenging ROS and by reducing ascorbate (Helena and Carvalho, 2008). It is therefore expected that tolerant plants may have higher scavenging ability relative to sensitive plants; hence more GSH, which contrasts with results produced by Abid et al. (2018). However, it was postulated, that tolerant cultivars, chiefly rely on upregulation of enzymatic antioxidation systems for ROS detoxification whereas the increase in GSH in sensitive cultivars might have been an attempt for the sensitive cultivars to exploit GSH (non-enzymatic) to mitigate oxidative stress.

Effect of abiotic stresses on carbohydrate concentration and soluble sugars

Carbohydrates are a major composition of food crops, key in the supply of energy for both humans and animals. Crop plants, particularly cereals, remain the major suppliers of carbohydrates, coming in various forms such as sugars, starches and fiber. For human nutrition, the type, rather than the amount of carbohydrates, is critical for health. In plants, several studies have indicated an increase in total soluble sugars concentration when subjected to stressful conditions. It is thought, that sugar transporters ferry sugars through plasma membranes and the tonoplast to adjust the osmotic pressure under stress conditions (Barnabás et al., 2008). In grains, it is postulated that abiotic stresses that perturb plant water status and carbon assimilation, such as a case of drought and salinity stress, elicit the conversion of stem reserves into soluble sugars and the mobilization of sugars into the grains during grain filling (Blum, 1998; Blum, 2005). Moreover, recent evidence suggests that xylem-borne abscisic acid (ABA) can be transported to plant reproductive structures and influence their development, presumably by regulating the gene expression that controls cell division and carbohydrate metabolic enzyme activity under drought conditions (Barnabás et al., 2008).

In a study by Abid et al. (Abid et al., 2018) severe water stress increased total soluble sugars (TSS) and fructose concentration. The trend of increase was more in tolerant plants relative to sensitive plants, suggesting a potential role of these sugars in alleviating water stress.

Moreover, after re-watering, both TSS and fructose concentration decreased, corroborating the suggestion. Recently, another study (Kim et al., 2017) has reported diurnal changes in starch and soluble sugars including sucrose, with soluble sugar contents tending to increase while starch decreased in response to drought stress, peaking during daytime. Similar results have also been obtained (Mostajeran and Rahimi-Eichi, 2009). To the contrary, starch levels remained comparatively low at the end of the day, hinting at a possibility that changes in sugar and starch levels may playa roleas important indicators for drought response associated with diurnal rhythms in rice (Kim et al., 2017). The decrease in starch might have resulted from the starch degradation pathway that was elicited by water stress as also observed from transcriptomic analysis in tomatoes by Egea et al. (Egea et al., 2018). In a wild relative of tomato, *Lycopersicum pennellii* upregulation of *Fructose Insensitive 1 (FINS1)* gene, which codes for a cytosolic fructose 1-6 bisphosphatase and down regulation of genes related to starch biosynthesis (ADG1) were also established under drought stress (Egea et al., 2018). This suggested that the tolerant tomato species prevents allocation of carbon towards starch synthesis and utilizes it for production of sugars.

Elevated carbon dioxide concentration (eCO_2), is one of the major consequences of climate change. Currently, plant survival, growth and productivity will be confronted with these increases, and hence it has emerged to be a key abiotic factor of interest in agriculture. Combined with other abiotic stresses, particularly drought, they may be particularly adverse on some crop plants. However, recent studies have unravelled that eCO_2 enhances drought tolerance in field pea plants through stimulated increases in total soluble sugars (Jin et al., 2014). This effect was particularly enhanced under increased phosphorus application, showing a significant linear relationship between leaf inorganic P (Pi) and TSS accumulation. It is hypothesized, that high Pi facilitates translocation of triose sugars from chloroplasts thereby enhancing sugar status of plant tissues (Abel et al., 2002; Rychter and Rao, 2005).

Presently, it is known that soluble sugars are an integral component of osmotic adjustment. Additionally, reports indicate that sugars play a role in enhancing the cellular antioxidation system (Bolouri-Moghaddam et al., 2010). This plausible relationship has been investigated and confirmed by Nishikawa et al. (2005), who reported that high soluble carbohydrate production in the florets of broccoli enhanced ascorbate synthesis, which facilitated partitioning of ROS in chloroplasts (Nishikawa et al., 2004). Also, upregulation of trehaloselevels, a carbohydrate storage molecule, by manipulating the intermediate trehalose-6-phosphate, conferred drought tolerance in transgenic rice plants, achieved through sugar-signalling and carbohydrate metabolism (Redillas et al., 2012).

The response: interventions and their effectiveness

At present time, billions of people are estimated to be micronutrient malnourished globally (Mason and Garcia, 1993). In order to sustain a healthy life, it is recommended that humans should consume 49 nutrients, failure of which results in chronic health challenges characterized by frequent and prolonged sickness, poor health, impaired development in children and consequently constraining both personal and national development (Branca and Ferrari, 2002; Grantham-McGregor and Ani, 1999). As such, efforts to increase nutritional status of food crops must be among key priorities, requiring a collaborative approach by various stakeholders. Coupled with the increased incidences of abiotic stresses associated with climate change, the need is even more exigent. While most abiotic stresses have been reviewed to increase micronutrients status in many food crops, they do adversely affect growth and yield, consequently reducing the amount of harvested food products available for consumption. This has led to a series of endless cycles of hunger and poverty, particularly in developing countries; for example, a case in Southern African countries such as Malawi following El Niño related drought effects. It is imperative, therefore, to consider elevating nutritional quality of food crops per unit of harvest, than to increase unit of harvest with limited nutritional quality.

Among the approaches to increase nutrient availability in an era of abiotic stresses may include increasing the resistance of key crop plants to maintain both nutritional quality and yield under abiotic stresses, or to simply increase their tolerance in order to maintain yield, though this may supply nutrients only minimally. Breeding, through both traditional techniques and genetic modification, is among promising tools for this aim. Various breeding criteria have been proposed for micronutrient rich staples (Welch and Graham, 2004), which include attainment of crop productivity or yield, significance of attained nutrient levels on human health, stability of the attained nutrient levels across a range of biotic and abiotic environments, proven bioavailability of the nutrients in humans and consumer acceptance. To our knowledge, numerous cases are reported on nutritionally enhanced food crops. Notable on the list include orange-fleshed sweet potato lines with high levels of β-carotene (over 200 µg/g). Also, beans with improved agronomic traits and grain type and 50 to 70% more iron have been bred through conventional means have been reported (Nestel et al., 2006). Prominently, release of golden rice (Beyer et al., 2002), a rice variety engineered to synthesize β-carotene in a way to address VAD remains amongst the largest of achievements and the noblest of pursuits in this regard. Achieved through insertion of a biosynthetic pathway de novo for synthesis of β-carotene, golden rice accumulate tremendously higher levels of carotene as a provitamin A (Beyer et al., 2002); a promising intervention particularly for developing countries. Recently, a yet new variant, golden rice 2 has been produced (Paine et al., 2005), producing 23 folds higher levels of β-carotene relative to the original Golden rice.

Moreover, nutritional enhancement is a potentially win-win approach, both for agriculture and human nutrition. Recently, improving micronutrient status in seeds of cereals has been investigated and found to enhance seed viability and seedling vigour through a more extensive and deep-rooting capacity, thus enhancing its ability to scavenge more effectively for needed nutrients, during micronutrient deficient edaphic conditions. In a trial in Bangladesh, biofortifying wheat grains for micro-nutrients increased wheat yield in nearly 80% of farmers' fields. Another study has also revealed that micronutrient dense seeds improve tolerance to both biotic and abiotic stress (Welch, 1986). In developed countries various success stories have been registered. Wheat varieties dense in zinc have been produced in Australia (Rengel and Graham, 1995), and have attained commercial success; In the US, iron deficiency in soils led to the development of a soybean cultivar with ability to grow and maintain high iron contents. Plants and humans have related sensitivities to micronutrient deficiencies. As such, plants low in micronutrients is usually susceptible to root diseases as previously confirmed (Graham and Rovira, 1984).

The question that arises is whether these interventions brought forth, have practical implications on health and their affordability coupled with acceptability. Indeed, various studies have been made to investigate the effects of biofortified foods on health of humans. For example, orange fleshed sweet potatoes, which have been bred for increased Vitamin A, significantly improved Vitamin A liver stores in primary school children (Van Jaarsveld et al., 2005). In another study, rice bred for high iron was found to improve serum ferritin concentrations and body iron levels in nonanemic women of reproductive age relative to control rice used locally (Haas et al., 2005). In a case of golden rice, it has demonstrated benefits beyond anticipated Vitamin A supplementation. Studies have revealed that Golden rice also supplies iron, derived from a gene from French beans which boosts iron content (Thomson, 2002). Moreover, it also contains a gene that inhibits the action of phytic acid on preventing iron absorption by the body (Gura, 1999). A prime concern that ought to be properly considered and addressed in many interventions relating to nutrient deficiency is cost effectiveness. An intervention must be duly acceptable by the target population and must be cost effective and affordable, devoid of which may render interventions unadoptable. In a study by Stein et al. (2006), it was established that introduction of Golden rice 2 as a way to combat VAD disease burden was considerably more cost effective relative to the traditional approach of using Vitamin A supplements.

Way forward: A summary of gaps and recommendations

It is established that abiotic stresses have an immense bearing on agricultural productivity and nutritional quality of food crops (Figure 3). The synergies between agriculture and nutrition have been well demonstrated and clearly revealed. As such, stakeholders must be willing to collaborate, and invest hugely in agriculture in order to achieve better nutrition for the growing population, particularly in developing countries. Africa, in particular, is a home for a myriad of unfortunate abiotic stresses; moreover, its inadequacy in resources and knowledge constrains its capacity to cope and adapt to these. However, notwithstanding these, Africa also remains a home of huge genetic diversity due to its subtropical – tropical climate, which can be harnessed for genetic improvement in key crops for food and nutritional security. At present, the advancements and interventions brought forth are promising. Plant breeding has been duly adopted as a reliable and effective tool for achieving nutritional quality. Besides, it has also proven effective in conferring abiotic stress tolerance in many crop species. Meanwhile, the breeding goal has been to either (1) improve tolerance to abiotic stress; or (2) to improve nutritional quality. But, do the breeding for these in isolation achieve both tolerance to abiotic stress and nutritional quality? For example, can producing a genetically engineered crop for drought tolerance produce a highly nutritious crop? Similarly, will a biofortifiedcereal crop be able to survive under abiotic stresses? Presently, most interventions have hardly addressed this phenomenon. Future efforts must thus seek to maintain higher nutritional quality in food products even in situations of environmental stresses. Moreover, this may not be a hard goal to achieve considering that most abiotic stresses increase synthesis of micronutrients (Tables 2 to 4). Some key nutrients for humans such as carotenes, amino acids, sugars and some micronutrients are part of an inherent defence system in plants' response to abiotic stress. This is among the reasons for increased nutrient content under abiotic stresses. Hence, it is highly likely that crops bred for tolerance to abiotic stresses, by enhancing key pathways for biochemical processes such as antioxidants, sugars and transporters for mineral elements, may achieve both tolerance and nutritional enhancement. A remaining concern, would be to optimize and achieve stability, yield, affordability and consumer acceptance. In such instances, an optimal intervention may require yield maintenance, palatability and marketability of the edible parts. In another twist, not all abiotic stresses have had a negative bearing on agriculture. Moreover, interactive effects of some abiotic stresses have ameliorated individual effects of others. For example, elevated carbon dioxide levels enhance drought tolerance; and this has been duly investigated in field grown peas. This was also coupled with increases in sugar levels, hence achieving both nutritional quality and drought tolerance. Presently, future efforts must consider assessing relative cost effectiveness, palatability, consumer acceptance and abiotic stress tolerance in nutritionally enhanced foods. Golden rice is an optimal example of an intervention that has been duly tested for its cost effectiveness, health impact and consumer acceptability, yet its abiotic tolerance has not been clearly investigated.

Conclusion

In total, our critical review demonstrates that agriculture and nutrition are inseparable. To our present knowledge, it is among the fewest studies, to comprehensively address issues and synergies of crop growth environmental factors and human nutrition. It has accentuated the intimacy between crop abiotic stresses and nutritional quality. Primarily, it reveals that abiotic stresses are a double-edged sword in agriculture, leaning more positively in nutritional quality and negatively on agricultural productivity (yield). Cognizant that the prime justification for agriculture is improvement of human wellbeing, with a particular focus on nutrition, factors that affect this pursuit require committed and solemn action. Notwithstanding, the auspicious interventions so far made using modern and traditional plant breeding tools, continued efforts are worthwhile, aimed at attaining both

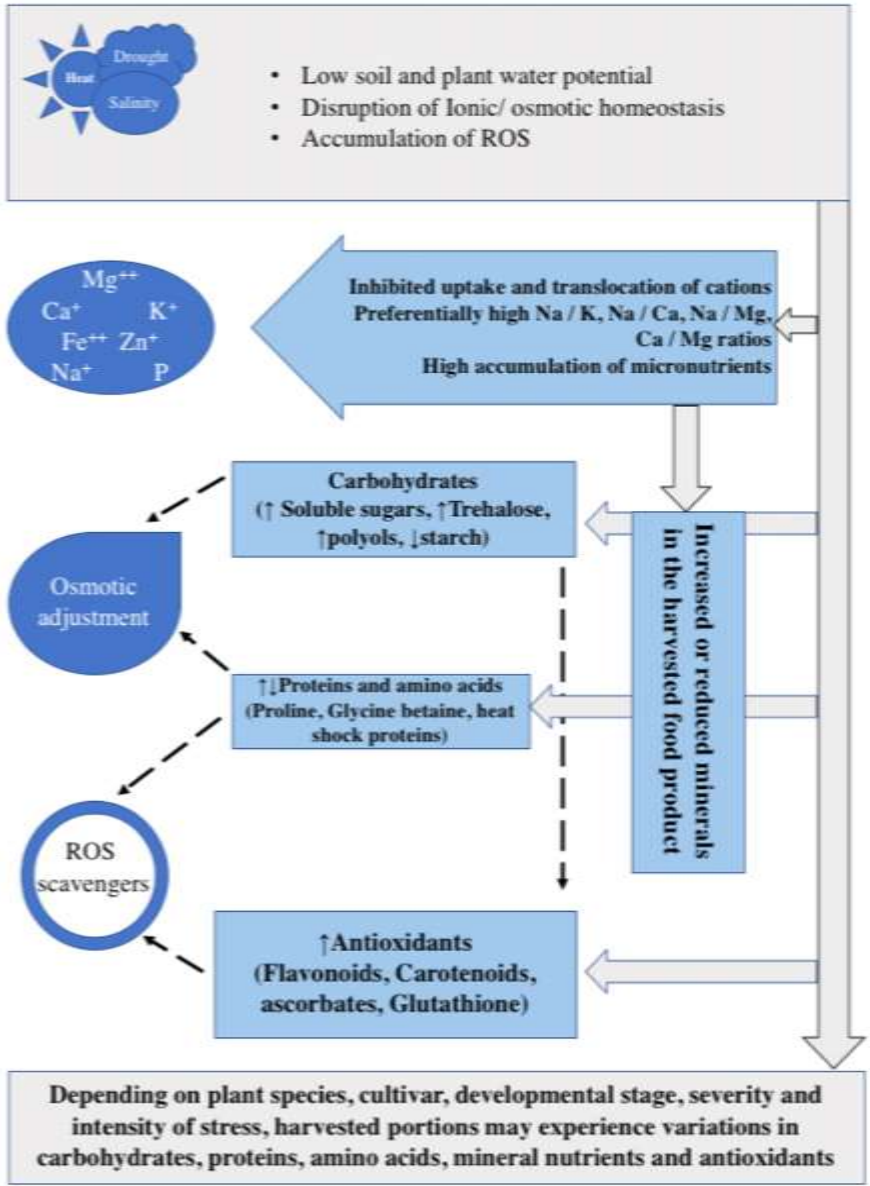

Figure 3. Effects of various forms of abiotic stresses on mineral nutrients, carbohydrates, proteins and antioxidants. Abiotic stress factors such as drought, salinity and heat, whether acting individually or synergistically, result into alterations in soil, and consequently plant water status. Salinity may disrupt ionic and osmotic homeostasis. Altogether, these stresses induce ROS production due to reduced photosynthetic capacity. Cumulative consequences of all these occurrences include changes in nutrient uptake, transport and distribution which affects final mineral status in harvested product, release of some soluble sugars, proteins and amino acids and antioxidants which aid in scavenging build-up of ROS and osmotic adjustments. The net effect on the final food product varies, depending on the sensitivity of the plant species, stage of development and severity of the stress.

abiotic stress tolerance and nutritional enhancement in one goal. It is imperative to explore more options and approaches towards addressing this complexity, as no single solution is apanacea in elevating crop nutritional status and yield in light of constraining environmental conditions. As scientists, researchers, farmers and development partners, we are therefore confronted with a hitch of an immense complexity and huge magnitude, calling for a multiplicity of approaches, multidisciplinary of teams and a convergence of knowledge and resources.

Table 3 . Effects of various crop abiotic stresses on mineral nutrient in harvested food crops.

Nutrient	Stress	Crop species	Effect ↑	Effect ↓	Effect —	Previous studies
Calcium	Drought	*Zea mays L. (Corn),*	√			Da Ge et al. (2010)
		*Solanumlycopersicum L (*Tomato)		√		Kamanga (Unpublished)
		Solanumlycopersicum L (Tomato)	√			Kamanga (2018)
	Salinity	*Cynaracarduculus* (Artichoke)		√		Francois et al. (1991); Francois (1995)
		Brassica rapa L (Chinese cabbage)		√		Osawa (1962)
Magnesium	Drought	*Zea mays L. (*Corn)	√			Da Ge et al. (2010)
		SolanumlycopersicumL (Tomato)		√		Kamanga (Unpublished)
		SolanumlycopersicumL (Tomato)	√			Kamanga et al. (2018)
		Daucuscarota (Carrot)		√		Sørensen et al. (1997)
Potassium	Drought	*Zea mays L.* (Corn)		√		Da Ge et al. (2010)
Phosphorus	Drought	*Zea mays L.* (Corn)	√			Da Ge et al. (2010)
Sodium	Drought	*Solanumlycopersicum* (Tomato)	√			Kamanga (Unpublished); Kamanga et al. (2018)
Zinc, Copper	Drought	*Zea mays L.* (Corn)	√			Da Ge et al. (2010)
Zinc, Iron, Copper	Ozone	*Zea mays L.* (Corn)	√			Garcia et al. (1983)
Potassium	Ozone	*Zea mays L.* (Corn)			√	Garcia et al. (1983)
	Ozone	*Solanum tuberosum L.* (Potato)	√			Piikki et al. (2007)
Magnesium	Ozone	*Zea mays L.* (Corn)			√	Garcia et al. (1983)
	Ozone	*Solanum tuberosum L.* (Potato)	√			Piikki et al. (2007)
Calcium	Ozone	*Solanum tuberosum L.* (Potato)			√	Piikki et al. (2007)
Phosphorus	Ozone	*Zea mays L.* (Corn)			√	Garcia et al. (1983)

(↑) abiotic stress increased mineral nutrient concentration: (↓) abiotic stress decreased mineral nutrient concentration; (—) abiotic stress did not cause any significant effect on mineral nutrient concentration.

Table 4. Effects of various crop abiotic stress factors on Antioxidants (Phenolics, Carotenoids, Ascorbates and Glutathione) and Carbohydrates.

Nutrient	Stress	Crop species	Effect ↑	Effect ↓	Effect —	Studies
Phenolics	HS, HL, CH	*Lactucasativa* (Lettuce)	√			Oh, Carey and Rajashekar (2009)
	Drought	*Solanum tuberosum L.* (Potato)	√			Andre et al. (2008)
		*Vitisvinifera (*Grape)	√			Deluc et al. (2009)
		Brassica napus (Oil seed)	√			Bouchereau et al. (1996)
	Salinity	*Brassica oleracea* (Broccoli)	√			Lopez-Berenguer et al., (2009)
		Rubusidaeus L. (Raspberry)	√			Neocleous and Vasilakakis (2008)
		Fragaria x ananassa (Strawberry)	√			Keutgen and Pawelzik (2007)
Ascorbate	Drought	*Solanum tuberosum L.* (Potato)	√			Noctor and Foyer (1998); Zushi and Matsuzoe (1998); Veit-Köhler et al. (1999)
		Daucuscarota (Carrot)	√	√	√	Sørensen et al. (1997)
	Salinity	*Brassica oleracea* (Broccoli)			√	Lopez-Berenguer et al. (2009)
	Salinity	*Rubusidaeus L.* (Raspberry)	√			Neocleous and Vasilakakis (2008)
	Salinity	*Fragaria x ananassa* (Strawberry)		√		Keutgen and Pawelzik (2007)
	Salinity	*Solanumlycopersicum* (Tomato)	√	√		Kim et al. (2008a)
	Heat	*Lactucasativa (*Lettuce)	√			Oh et al. (2009)
Carotenoids	Drought	*Daucuscarota* (Carrot)	√	√	√	Sørensen, et al. (1997)
		Triticumaestivum L. (Wheat)		√		Abid et al. (2018)
		Solanum tuberosum L. (Potato)	√	√	√	(Andre et al., 2008)

Table 4. Contd.

		Solanum tuberosum L. (Potato)	√		√	Zushi and Matsuzoe, (1998); Favati et al., (2009)
	Salinity	*Lactucasativa* (Lettuce)	√			Kim et al. (2008a)
Glutathione	Drought	*Triticumaestivum L.* (Wheat)	√			Abid et al. (2018)
Carbohydrates						
TSS	Drought	*Triticumaestivum L.* (Wheat)	√			Abid et al. (2018)
		Oryza sativa L. (Rice)	√			Kim et al. (2017); Mostajeran and Rahimi-Eichi (2009)
		Solanumlycopersicum (Tomato)	√			Egea et al. (2018)
	eCO_2	*Pisumsativum* (Field pea)	√			Jin et al. (2014)
Starch	Drought	*Oryza sativa L.* (Rice)		√		Kim et al. (2008b)
		Solanumlycopersicum (Tomato)	√			Egea et al. (2018)

(↑) abiotic stress increased antioxidant / carbohydrate concentration: (↓) abiotic stress decreased antioxidant / carbohydrate concentration; (—) abiotic stress did not cause any significant effect on antioxidant / carbohydrateconcentration.

CONFLICT OF INTERESTS

The authors declare that they have no conflict of interest.

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