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Review

Ability of Nutrient Management and Molecular Physiology Advancements to Overcome Abiotic Stress: A Study on Sub-Saharan African Crops

Koffi Pacome Kouame [1], Raj Kishan Agrahari [1], Noren Singh Konjengbam [2], Hiroyuki Koyama [1] and Yuriko Kobayashi [1,*]

[1] Faculty of Applied Biological Sciences, Gifu University, Gifu 501-1193, Japan; kouamekoffifrance@gmail.com (K.P.K.); kishan.agrahari016@gmail.com (R.K.A.); koyama.hiroyuki.i9@f.gifu-u.ac.jp (H.K.)
[2] College of Post Graduate Studies in Agricultural Sciences, Central Agricultural University (Imphal), Umiam 793103, India; norensingh27@gmail.com
* Correspondence: kobayashi.yuriko.h8@f.gifu-u.ac.jp

Abstract: Abiotic stress is a major cause of the declining crop yield worldwide, especially in tropical agricultural areas. Meeting the global food demand has become a serious challenge, especially in tropical areas, because of soil acidity, Al and Fe toxicity, drought and heat stress, and climate change. In this article, we reviewed several research and review papers from Google Scholar to list the different solutions available for the mitigation of abiotic stress, especially in tropical regions where several major crops, such as maize, sorghum, wheat, rice, soybean, and millet, are affected by abiotic stress and fertilizer input. In particular, Sub-Saharan Africa (SSA) has been affected by the low use of fertilizers owing to their high cost. Therefore, soil and plant researchers and farmers have developed many techniques to mitigate the effects of stress and improve the crop yield based on the agroecological zone and crop type. Nutrient management using chemical fertilizers alone or in combination with organic crops is a strategy recommended to cope with abiotic stress and increase the crop yield, particularly in developing countries. Notably, integrated soil fertility management has been effective in semi-arid areas under drought and heat stress and in subhumid and humid areas with high soil acidity and Fe toxicity in Africa. Recent advances in the molecular physiology of various crops considered a staple food in SSA have facilitated the breeding of transgenic tolerant plants with high yield. However, the feasibility and implementation of this technique in the African continent and most tropical developing countries are major issues that can be solved via adequate subsidies and support to farmers. This review can aid in the development of novel strategies to decrease hunger and food insecurity in SSA.

Keywords: abiotic stress; acid soil; Al toxicity; crops; drought; fertilizer; heat; SSA

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1. Introduction

The global population is estimated to reach approximately 10 billion by 2050 [1,2]. However, many challenges, such as food insecurity, abiotic stress, and increased pest outbreaks, attributed to climate change demand global attention, particularly in tropical regions [3]. Approximately 50% of the global population lives in tropical regions, and more than two-thirds live in extreme poverty [4]. However, in recent years, this situation has been exacerbated by the continuous decline in crop yield owing to increased abiotic stress [4]. The Food and Agriculture Organization (FAO) has emphasized the need for a 50% increase in food production to meet the rising demand by adopting sustainable farming practices [5,6]. The efficient management of nutrients and irrigation using seeds of high-yielding crop varieties will be necessary to meet the increasing food demand in tropical regions and promote green agriculture.

The use of high-yield crop varieties, inorganic fertilizers, irrigation systems, and synthetic pesticides has substantially enhanced crop productivity in various Asian and developed countries. These agricultural practices have played a vital role in meeting the increasing food demand to ensure sufficient food supply [7,8]. Many studies have focused on the detrimental effects of these practices on surface and groundwater pollution in Asia [9–11] and Europe [12]. Among the developing countries, Sub-Saharan Africa (SSA), which accounts for 13% of the total arable land worldwide [13], is characterized by various factors, such as limited fertilizer availability, high soil acidity [14–16], drought, water stress [17], and nutrient deficiency [18]. The International Fertilizer Association has strongly emphasized the critical role of fertilizer inputs in promoting food production and ensuring food security in Africa [19–22]. However, the adverse effects of pesticide misuse, excessive reliance on synthetic inputs, abiotic stress, and climate change in the tropical regions of both developed and developing countries have raised concerns [23]. Therefore, proactive and emergency strategies that prioritize green, efficient, and sustainable agricultural practices are necessary to ensure food security for future generations.

Over the past decade, studies have focused on the use of organic compounds to promote sustainable agriculture while mitigating the ecological consequences of increasing global food demand [24–26], especially in tropical regions [27]. Consequently, alternative strategies based on research findings in the fields of plant nutrition, climate change, and molecular physiology have been developed for different geographical areas, especially tropical regions. The synergistic application of inorganic and organic compounds can increase the crop yield [7,28,29]. Several studies have elucidated the molecular mechanisms underlying various stresses, such as drought [30], high temperature [31], and soil acidity [32–34]. These findings offer valuable insights on plant nutrient management, fertilizer use, and molecular breeding to enhance the agricultural yield in tropical regions.

This review provides comprehensive information on the various abiotic stresses affecting tropical crops, with a particular focus on soil acidity, Al and Fe toxicity, drought and heat stress, and climate change. Furthermore, this review highlights the recent advancements in plant nutrient management and the molecular breeding strategies used to enhance crop yields, fortify sustainable agricultural practices, and ensure food security.

2. Effects of Abiotic Stress on Nutrient Imbalance and Crop Yield

Abiotic stress, namely soil acidity, Al and Fe toxicity, drought and heat stress, and climate change, pose serious environmental challenges that affect and reduce the production of crops worldwide [35]. Crop yields are expected to reduce owing to climate change and the side effects of the increased world population that force the extension of urban areas, thereby limiting agriculture to areas less appropriate for crop cultivation [36]. Among various abiotic stresses, soil acidity, drought, elevated temperatures, and salinity are recognized as the predominant limiting factors [37]. These stresses, in combination with climate change and the emergence of new pests and diseases, have a significant effect on global agricultural production, particularly in tropical regions [38]. Abiotic stresses frequently induce morpho-anatomical and physiological growth constraints, further exacerbating challenges in crop production [39]. Soil acidity, heat stress, drought, and climate change are the most critical limiting factors for maize (*Zea mays*), millet (*Panicum milliaceum*), and sorghum (*Sorghum bicolor*) production, but not cassava (*Manihot esculenta*), which is mainly limited by floods in SSA [40]. In this article, we aimed to outline the adverse effects of these factors, specifically focusing on their impact on tropical crops.

2.1. Al and Fe Toxicity

Soil acidity, characterized by a pH level of ≤ 5.5, is a significant constraint to crop production worldwide [41]. This condition is particularly prevalent in tropical and subtropical regions [42,43]. The primary challenge associated with acidic soils is the toxicity of aluminum (Al^{3+}), phosphate (${PO_4}^{2-}$), and iron (Fe^{2+}), which can have detrimental effects on the plant [32,44,45]. This phenomenon adversely affects crops, such as sesame (*Sesamum* *indicum*), and impedes nutrient mineralization [43]. It also affects other vegetable crops, such as *Brassica juncea*, *Phaseolus vulgaris*, *Pisum sativum*, and *Vigna mungo* [46]. This phenomenon affects approximately 600 Mha of land in SSA [14]. In South America, particularly Brazil, soil acidity affects approximately 205 Mha of land [47].

In the tropics, Al toxicity affects 25–80% of crop production [48]. The detrimental effects of Al^{3+} are manifested in developing root tips, as they disrupt crucial processes related to cell division, elongation, and genotoxicity. This disturbance ultimately leads to the inhibition of root growth, hindering the ability of crops to extend their roots for nutrient uptake [32,34]. In SSA, Al significantly decreases the yields of several crucial crops (Table 1). For example, in Ethiopia, Al reduces the grain yield of wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare*), and beans (*Phaseolus vulgaris* L.) [49]. Across SSA, elevated soil acidity can trigger various indirect consequences. These include the suboptimal nodulation of legumes, the proliferation of acid-tolerant weeds, stunted root growth, and a reduction in the yields of various crops, such as millet, sorghum, tomato (*Solanum lycopersicum*), sweet potato (*Ipomoea batatas*), and tea [50,51]. Soil acidity also reduces enzymatic activity, interrupts microbially mediated nutrient cycling, and hampers microbial activity [52,53]. These constraints vary depending on the degree of acidity [54]. For instance, wheat [54], maize, and canola [55,56] exhibit yield-specific responses to soil pH. Moreover, Al reduces nitrogen (N) uptake and decreases N use efficiency (NUE) and water use efficiency (WUE) in crops such as maize [57], reducing its yield and contributing to high drought stress and nutrient unavailability due to root growth inhibition [46]. In high-income economies, the widespread application of lime to enhance the soil pH has led to remarkable increases in crop yields over the past century [58–61]. In contrast, low-income economies, particularly those in tropical and subtropical regions, face significant challenges. Extreme poverty often prevents farmers from producing lime to ameliorate soil acidity and boost crop yields [41]. Furthermore, these regions are characterized by iron toxicity, which causes severe damage to rice (*Oryza sativa*).

Table 1. Major crops sensitivity level to abiotic stresses in Sub-Saharan Africa.

Abiotic Stresses	Major Crops	References
Soil acidity and Al Toxicity	Sensitive	
	Barley	[27]
	Maize	[62]
	Wheat	[38]
	Soybean, Peanut	[48]
	Less sensitive	
	Pineapple, Sweet potato,	[48]
	Cassava, Yam	[50]
Fe toxicity	Rice (lowland)	[63,64]
Heat and drought	Sensitive	
	Soybean, Peanut	[65,66]
	Wheat	[67]
	Barley	[68]
	Rice	[64]

Table 1. *Cont.*

Abiotic Stresses	Major Crops	References
	Less sensitive	
	Yam, Cassava	[69]
	Sweet potato	[70]
	Sorghum	[71]
	Finger Millet	[72,73]
Climate change	Sensitive	
	Maize, Rice	[74]
	Wheat	[67]
	Barley	[75]
	Less sensitive	
	Cassava, Millet, Sweet potato	[74,76]
	Sorghum	[75]

Iron toxicity is another major factor that significantly limits crop yields, particularly rice production in West Africa (Table 1). In comparison to Asia, rice production in SSA faces significant challenges arising from additional factors, such as nutrient deficiencies, low base cation exchange, a low nutrient-holding capacity, and high levels of phosphorus fixation [63,77]. Iron toxicity is characterized by physiological indicators, such as leaf chlorosis and necrosis, leading to yield reductions ranging from 10% to 100% [78,79]. Excessive iron uptake and its subsequent accumulation in leaves occur when soil iron concentrations exceed the critical threshold of 500 mg Fe kg^{-1} [80]. This phenomenon is linked to the development of symptoms of iron toxicity, commencing as brown spots at the leaf tip and advancing to purple, reddish-brown, or yellow discoloration. Ultimately, the affected leaves desiccate, giving the plant a scorched appearance. Concurrently, the root architecture becomes dark brown and weakened [81]. The risk of Fe toxicity is notably high in regions characterized by high rainfall, such as sub-humid and humid zones [77], owing to the poor management of water, crops, and mineral fertilizers [81]. In semi-arid zones, the situation deviates because of the co-occurrence of drought and heat stress, which overlaps with the prevalence of Fe toxicity, ultimately resulting in reduced rice yields [82].

2.2. Drought and Heat Stress

Drought and heat stress are two major abiotic stresses that can occur simultaneously and severely affect crop growth and productivity, especially in arid and semi-arid zones [83–85]. Although extensive research has been conducted on drought and heat stress individually [86–90], their combined effects are gaining increasing scientific relevance because of climate change-induced water scarcity.

Several staple African crops, such as cassava (*Manihot esculenta*), potatoes (*Solanum* spp.), sweet potatoes (*Ipomoea batatas*), yams (*Dioscorea* spp.), and plantains (*Musa* spp.), have adverse effects on yield due to rising temperatures and the prolonged effects of climate change-induced drought (Table 1). Drought affects nearly 80% of agricultural land, imposing limitations on global yield and crop production in both temperate and tropical regions [65,91,92]. The impact of drought on cereal production has been particularly severe [93]. Recent studies have shown that the combined effects of drought and heat are more severe on maize, barley, and sorghum yields than either stress alone [85]. Moreover, drought and heat stress are affected by climate change.

Climate change is projected to have a significant impact on crop yields in the tropics, particularly in West Africa, where the projected temperature rise of 2.1 °C could severely reduce the maize yield in dry lowlands and lowlands (Table 1). Drought has been established in numerous tropical areas as a factor that leads to decreased crop yields, affecting crops, such as wheat, cowpeas (*Vigna unguiculata*) [93], millet [94], and cassava [69,95]. For instance, up to 84.27% of cassava mortality has been attributed to drought stress [96]. Furthermore, climate change, primarily through drought stress, is recognized for its adverse impact on maize, groundnut [97], and bean yields, as well as on their nutritional quality [98,99]. In SSA, the limited response of major staple crops, such as maize, soybean (*Glycine max*), sorghum, rice, and cassava, to chemical fertilizers, possibly due to soil acidity, drought, and heat stress, presents a substantial challenge (Table 1). Therefore, optimizing crop nutrient management through fertilizer application (both inorganic and organic) while mitigating stress factors such as Al^{3+} and Fe^{2+} toxicity, drought, and heat stress [100] is crucial.

3. Nutrient Management under Abiotic Stress: Combined Use of Inorganic and Organic Fertilizers

3.1. Effects of Organic and Inorganic Fertilizers on Nutrient Availability

The application of organic fertilizers, whether used in conjunction with chemical fertilizers or as a discrete method, has demonstrated efficacy in mitigating soil acidification and enhancing soil fertility [100,101]. For example, the incorporation of pig manure and straw as amendments in maize and wheat has been found to enhance the immobilization of abiotic NH_4^+-N and NO_3^--N by increasing the soil carbon content. Notably, manure application independently ameliorated soil acidity, whereas straw amendment did not yield a comparable effect [102]. In tobacco (*Nicotiana tabacum*) cultivation, cow manure, whether discrete or combined with synthetic fertilizer in acidic soil, significantly reduced the soil exchangeable acid content, with a substantial 51.28% reduction in exchangeable Al^{3+} when organic matter was applied, thereby mitigating soil acidification [103]. This practice further led to a 37.19% and 42% increase in exchangeable base cations for cow manure and the combined organic–inorganic fertilizer, respectively, compared to the discrete use of chemical fertilizer. The use of mixed poultry manure (50%) + NPK (50%) or 100% poultry manure significantly elevated the soil pH, cation exchange capacity (CEC), and NPK uptake compared with 100% synthetic NPK [104] (Table 2). Conversely, the incorporation of crop residues has demonstrated a high potential to alter soil CEC, organic carbon levels, P, K, and pH [105]. Most studies conducted in Asia have revealed the importance of combining organic and inorganic fertilizers to mitigate environmental stresses, such as water pollution, soil acidity, and plant nutrient deficiency. However, reports indicate that the levels of chemical fertilizers and organic inputs for nitrogen supply are significantly lower in Africa than in Europe and North America [106]. Taken together, it is important to highlight trends in nutrient management to mitigate environmental stress in Africa.

Table 2. Evaluation of different types of fertilizer application depending on crops in SSA.

AEZ	Crops	Fertilizer Use
Semi-arid zone	**Cereals** maize (*Zea mays*), millet (*Panicum milliaceum*), sorghum. (*Sorghum bicolor*), soybean (*Glycine max*), bean (*Phaseolus vulgaris* L.), wheat (*Triticum aestivum* L.) pigeon pea (*Cajanus cajan*) **Root tubers** cassava (Manihot esculenta) **Perennial crops** cotton (*Gossypium herbaceum*)	SI+N [107] CA+mulch+Manure [108] Manure [109] Biological N-fixation (*Acacia mangium*) [110] Urea/DAP/TSP/KCl [111] NPK [112] Sulfur(S) [113] ISFM [114]

Table 2. *Cont.*

AEZ	Crops	Fertilizer Use
Sub-humid zone	**Cereals** rice (*Oryza sativa*), maize (*Zea mays*), millet (*Panicum milliaceum*), sorghum (*Sorghum bicolor*), soybean (*Glycine max*), bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata*) **Root tubers** cassava (*Manihot esculenta*), yam (*Dioscorea alata*), sweet potato (*Ipomoea batatas*), groundnut (*Arachis hypogaea*) **Perennial crops** cotton (*Gossypium herbaceum*), cashew nut (*Anacardium occidentale*), cocoa (*Theobroma cacao*), coffee (*Coffea canephora*), sugar cane (*Saccharum officinarum*),	Lime and Gypsum [115–117] NT+NPK/CT+NPK+Manure/ NT+NPK+Manure) [118–120] Biochar [121] NPK+Ca+Zn+B/N+Manure [122,123] Biological N-fixation (*Acacia mangium*, *Casuarina equisetifolia* [110] ISFM [124–127] NPK/Urea/DAP/TSP/KCl/ISFM [111] INPM [114,128]
Humid zone	**Cereals** rice (*Oryza sativa*), maize (*Zea mays*) wheat (*Triticum aestivum* L.) sweet potato (*Ipomoea batatas*) **Root tubers** cassava (*Manihot esculenta*), yam (*Dioscorea alata*) **Perennial crops** rubber tree (*Hevea brasiliensis*), oil palm tree (*Elaeis guineensis*), cocoa (*Theobroma cacao*), coffee (*Coffea canephora*), plantain banana (*Musa paradisiaca*), desert banana (*Musa acuminata*), mango (*Mangifera indica*), avocado (*Persea americana*), ananas (*Ananas comosus*)	Lime and Gypsum [115–117,129] INPM [114,128] Crop residue [130]

3.2. Crop Responses to Fertilizer Management Practices in SSA

In SSA, the implementation of Integrated Soil Fertility Management (ISFM), which strategically combines organic and inorganic fertilizers, is progressively recommended for African agricultural practices across distinct agroecological zones [124,127,131,132]. ISFM is an approach aimed at enhancing crop yields and sustaining long-term soil fertility by strategically combining fertilizers, recycled organic resources, responsive crop varieties, and improving agronomic practices [51]. In semi-arid zones, where drought and heat stress are severe, plant nutrient management differs significantly from that in sub-humid and humid regions [133,134] (Table 2). ISFM enhances N and P efficiency in maize by 54 and 16%, respectively [135]. The combination of organic input and urea for maize cultivation led to a 64% increase in N uptake and an 84% increase in yield, while the synergistic effects of both (organic input and urea) nearly doubled the yield to 114% [128]. Studies conducted in Ethiopia have demonstrated that the simultaneous application of inorganic and organic fertilizers yielded significantly higher crop production in tropical agroecosystems than using either fertilizer alone. Furthermore, they concluded that the synergy between manure and NP fertilizer, coupled with practices, such as crop rotation, green manuring, and crop residue management, resulted in substantial increases in wheat and faba bean grain yields, emphasizing the economic incentives for farmers to adopt ISFM practices [136]. For example, the yields of maize and sorghum were significantly enhanced by the co-application of NPK, manure, and micronutrients in Mali, Kenya, Nigeria, and Tanzania [136]. The efficient uptake of N and P owing to an increase in soil organic matter (SOM) has also been reported in southern Nigeria [136,137]. Furthermore, the utilization of local fertilizers, such as crop residue application, and the implementation of techniques such as mulching or straw application [138] have been shown to notably mitigate soil temperature and drought stress, resulting in enhanced crop yields (Table 2). Recently, African agronomists have emphasized the use of blended fertilizers, such as NPK+S or NPK+Zn, to enhance rice yield [139]. This approach is driven by the potential of certain compounds, such as sulfur (S), to significantly increase agronomic N-use efficiency [140]. This approach may be because of S, Si, Zn, and P deficiencies in most West African countries [141–143].

In sub-humid and humid zones, a substitutive approach for ISFM is strongly recommended. This approach involves the application of 50% of the recommended inorganic N or P combined with total manure [125,135] (Table 2). This practice is recommended to compensate for the loss of organic matter and soil nutrients [144]. For example, crop N uptake can be enhanced by 26% by combining synthetic N with manure in maize cultivation [144]. Seasonal variations in crop production, climate change, and abiotic stresses have led researchers, farmers, and governments to diversify organic fertilizer sources, provide guidance, and offer fertilizer subsidies (Figure 1). The utilization of a rock-based fertilizer (phosphate rock) in conjunction with compost resulted in enhanced Maize and Soybean yields of 2.5 t·ha^{-1} during both the dry and rainy seasons. Similarly, Yam yields increased to 2.5 t·ha^{-1} during the rainy season and 3.0 t·ha^{-1} during the dry season [145]. In Nigeria, rock phosphate combined with poultry manure increased the P content and yield of maize and cowpea [146]. Furthermore, N, P, and K uptake was significant in sorghum in the presence of combined rock phosphate and farmyard manure [147]. Sustainable agricultural productivity can be improved through effective disease management, optimized soil and water resources, the use of organic fertilizers, the utilization of new tools and facilities (Figure 1), and the adoption of improved plant varieties with good-quality seeds from traditional or biotechnological sources, including transgenic breeding. Transgenic varieties are considered a promising approach for doubling or tripling African crop yields [70,148]. However, their successful utilization for abiotic and biotic stress tolerance requires a clear understanding of the molecular physiological mechanisms related to stresses, such as Al and Fe toxicity, nutrient deficiency, drought, and heat stress, whether occurring individually or in combination, within specific crop species.

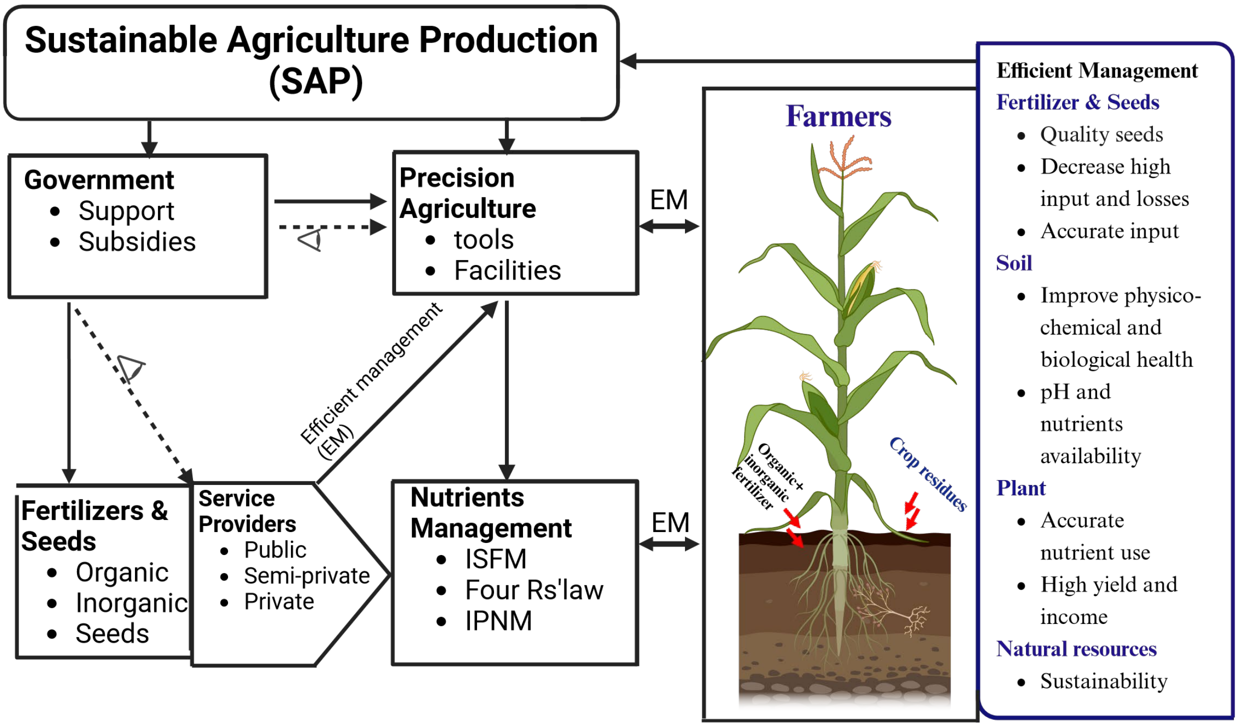

Figure 1. Model for sustainable agricultural production adapted for tropical regions, especially in Sub-Saharan Africa. ISFM, integrated soil fertility management; IPNM, integrated plant nutrition management; EM, efficient management. The Four Rs' Law (right time, right source, right rate, and right place) in fertilizer input indicates the practices that must be promoted (black arrow) and supervised (dotted arrow) by the government through private, public, and semi-private sectors to ensure food security. Farmers can also co-operate with these sectors for sustainable crop production.

4. Molecular and Physiological Mechanisms of Abiotic Stress

In this section, we explore the molecular and physiological mechanisms developed by plants to alleviate Al toxicity and cope with drought and heat stress. Additionally, we provide examples of major crops cultivated in tropical regions that hold potential for the future molecular breeding of crop varieties.

4.1. Molecular and Physiological Mechanisms Underlying Al Stress

It has been observed that the mechanisms regulating Al tolerance are different in various phytospecies under Al stress conditions [149]. In some species, various mechanisms can function simultaneously to generate Al resilience through their combined effects. Although the type of tolerance generation mechanism for Al^{3+}-induced phytotoxicity remains controversial, Al exclusion mechanisms are widely accepted to be involved in Al^{3+} detoxification [150]. However, the molecular and physiological mechanisms underlying Al phytotoxicity have been extensively studied, primarily utilizing model plants, such as *Arabidopsis*, and important crops such as wheat and rice [30,32,151,152]. Based on these studies, two primary categories of plant tolerance mechanisms have been proposed to mitigate the toxic effects of Al: "Exclusion" and "Internal Al tolerance" [153,154]. In the context of Al, exclusion mechanisms are characterized by their capacity to reduce the presence of rhizotoxic Al ions (Al^{3+}) within the symplasm of plant cells, whereas internal tolerance mechanisms effectively mitigate Al toxicity and damage within the cytosol. Furthermore, additional mechanisms have been identified, such as the alteration of rhizosphere pH, Al efflux across the plasma membrane [152], and the removal of Al by the sufficient application of calcium at the plasma membrane surface, which creates a negatively charged screen between Al and the plasma membrane [155].

Numerous studies have provided evidence supporting the Al exclusion mechanism, that is, the excretion of organic acids (OAs) that effectively chelate Al^{3+} toxic ions in various plants, including staple food crops commonly grown in tropical regions. This phenomenon is mediated by specific transporters for OAs, such as aluminum-activated malate transporter1 (ALMT1), which is encoded by the *ALMT1* gene in wheat [156]. This gene has been characterized in several other plants and crops (Table 3), including *AtALMT1* in *Arabidopsis* [157], *BnALMT1* and *BnALMT2* in rapeseed (*Brassica napus*) [158], and *VrALMT1* in mung beans (*Vigna radiata*) [159]. In addition, similar patterns of Al-activated citrate transporter genes from the multidrug and toxic compounds extrusion (MATE) family, such as HvAACT1 [160] and SbMATE [161,162], have been observed, with their constitutive expression reported for the first time in barley (*Hordeum vulgare*) and sorghum (*Sorghum bicolor*). Moreover, citric acid has been shown to have a strong affinity for Al and enhance phosphorus availability from insoluble Al phosphate in snap beans (*Phaseolus vulgaris* L.) [163]. Recently, several *MATE* family genes associated with citrate secretion have been identified in various crops, including maize (*Zea mays*), rice (*Oryza sativa*), peanut (*Arachis hypogaea*), and soybean (*Glycine max*) (Table 3). Studies in *Arabidopsis* have provided strong evidence that the expression of *AtALMT1* and *AtMATE* is regulated by several transcription factors [155,164]. A notable example is the involvement of the master regulator SENSITIVE TO PROTON RHIZOTOXICITY1 (STOP1), which has been identified as a key regulator of the Al-inducible expression of both *AtALMT1* and *AtMATE* under Al stress [165–167]. In contrast, STOP1 was highly conserved among plants [168]. Recently, it was suggested that SbSTOP1 in Sorghum activates the transcription of the β-1,3-glucanase, which reduces callose deposition under Al toxicity [169]. In addition to its role in the Al stress response, STOP1 has demonstrated pleiotropic regulation under various stresses, such as salt, drought, hypoxia, low pH, and nutrient management [170,171]. For example, in maize, ZmSTOP1 plays a crucial role in drought tolerance by exhibiting hypersensitivity to abscisic acid (ABA) treatment in the roots and insensitivity to stomatal hormones, consequently promoting stomatal closure [172]. Therefore, STOP1 is a useful genetic factor for alleviating Al stress and other growth-limiting factors. Therefore, further studies should analyze the STOP1-mediated environmental stress tolerance in various crops.

Table 3. Transporters responsible for Al-responsive organic acid secretion from roots in various plants.

Plant Species	Organic Acid Transporter	Reference
Malate secretion		
Triticum aestivum	TaALMT1	[156]
Arabidopsis thaliana	AtALMT1	[157]
Brassica napus	BnALMT1, 2	[158]
Secale cereale	ScALMT1	[173]
Medicago sativa	MsALMT1	[174]
Holcus lanatus	HlALMT1	[175]
Vigna radiata	VrALMT1	[159]
Citrate secretion		
Sorghum bicolor	SbMATE	[161]
Hordeum vulgare	HvMATE (HvAACT1)	[160]
Arabidopsis thaliana	AtMATE	[176]
Phaseolus vulgaris	MATE-a, -b	[177]
Secale cereale	ScMATE2 (ScFRDL2)	[178]
Zea mays	ZmMATE1, ZmMATE6	[179,180]
Oryza sativa	OsFRDL4, OsFRDL2 (OsMATE2)	[181,182]
Eucalyptus camaldulensis	EcMATE1	[183]
Triticum aestivum	TaMATE1B	[184]
Vigna umbellata	VuMATE1	[185]
Brassica oleracea	BoMATE	[186]
Amaranthus hypochondriacus	AhMATE1	[187]
Fagopyrum esculentum	FeMATE1	[188]
Medicago truncatula	MtMATE66	[189]
Populus trichocarpa	PtrMATE1	[190]
Brachypodium distachyon	BdMATE	[191]
Cajanus cajan	CcMATE1	[153]
Glycine soja	GsMATE	[192]
Glycine max	GmMATE75, 79, 87, GmMATE13	[193,194]
Arachis hypogaea	AhMATE (AhFRDL1)	[195]
Oxalic secretion		
Hevea brasiliensis	HbOT1, 2	[196]
Al-responsive transcriptome		
Populus tremula	MATE	[197]
Camellia sinensis	MATEs, ALMTs, CsMATE1,CsALMT1	[190,198]
Citrus sinensis	MATEs, ALMTs	[199]
Stylosanthes	MATE family	[200]
Nicotiana tabacum	NtMATE	[201]
Populus trichocarpa	PoptrALMT10, 54	[202]
Solanum lycopersicum	SlALMT3	[203]
Saccharum officinarum	ALMT2,4,5,7,9,11	[162]
Lens culinaris	ALMT-1, MATE-a,b,c	[204]
Triticum aestivum	TaMATE85,100,114	[205]
Cicer arietinum	CaMATE2,4	[206]
Chenopodium quinoa	CqALMT6	[207]

4.2. Drought and Heat Stress

4.2.1. Physiological Adaptation

Abiotic stresses, such as high temperatures and water deficits, can adversely affect plant growth and development, resulting in irreversible declines in crop yields [28,208,209]. According to the Intergovernmental Panel on Climate Change [210], the synergistic effects of drought and heat stress are expected to increase. Consequently, it is crucial to gain a comprehensive understanding of the mechanisms utilized by plants to respond to both stresses. Drought-induced molecular physiological dysfunctions include stomatal closure, oxidative stress, reduced photosynthesis the, disruption of cell walls, and a reduction in root length and plant growth [90,211]. Numerous plant species have developed multiple mechanisms, including the alternative oxidase (AOX) [212], to mitigate or withstand drought stress [213,214]. This stress triggers the activation of numerous genes and transcription factors, leading to the synthesis of a wide array of proteins and enzymes [211,215–218]. Extensive research has been conducted on diverse plant species, including *Arabidopsis* [83,219], wheat [220], barley [221], and tobacco [82], to investigate their responses to combined drought and heat stress, as well as their individual responses to each stress condition. These studies revealed similar physiological responses, with more severe damage being observed in plants exposed to both stresses than in those subjected to a single stress. These findings highlight the existence of shared defense mechanisms among these plant species in response to drought and heat stress [222]. In this section, our primary emphasis is on the prominent crops cultivated in tropical regions, highlighting the molecular and physiological mechanisms that have evolved to mitigate the combined effects of drought and heat stress.

Plants adopt three primary strategies for coping with drought stress: escape, avoidance, and tolerance [223]. Avoidance involves stomatal closure, reduced photosynthesis, enhanced respiration, and suppressed transpiration to maintain the plant's water status and prevent water loss [82]. For example, morphophysiological mechanisms in maize and sorghum under heat or drought stress are characterized by leaf wax, a lower leaf angle, compact tassels, and a lower cob angle, all of which aim to prevent evapotranspiration [224,225]. An important physiological adaptation in plants is the increase in photosynthetic rates. The maintenance of optimal photosynthetic activity contributes to membrane stability and enhances heat tolerance [226]. Moreover, stomatal conductance is significantly reduced under both stress conditions in *Arabidopsis* and citrus plants [83,219]. Plants exhibit time-dependent responses to both drought and high temperatures. Initially, low levels of reactive oxygen species (ROS), such as H_2O_2 and O_2^-, are observed within the first 24 h, accompanied by an increase in antioxidant enzyme activity. However, at later time points (after 24 h), ROS levels increase substantially, while the antioxidant enzyme activity gradually decreases, potentially indicating the disruption of the antioxidant pathway [227]. Stress-dependent ROS detoxification mechanisms are also observed with heat-stress-inducing cytosolic ascorbate peroxidase (APX) and thioredoxin peroxidase (TPX), whereas drought stress leads to an increase in catalase (CAT) and glutathione peroxidase activities. However, a combination of these stresses uniquely induces glutathione S-transferase (GST), glutathione reductase (GR), copper–zinc superoxide dismutase (CuZnSOD), AOX, and glutathione peroxidase (GPX) enzymes [228].

4.2.2. Molecular Mechanism

Transcriptomic analyses of several plants under drought and heat stress have revealed many transcripts [82,83,222] involved in mitigating these stresses. For example, the transcriptome of sorghum under combined drought and heat stress revealed 5779 transcripts (3003 upregulated and 2776 downregulated). Gene ontology analysis revealed enrichment in categories related to lipid localization, the regulation of photosynthesis, fluid transport, and protein folding. Importantly, these enriched categories overlapped with the responses observed under drought or heat stress [229]. Moreover, a unique set of genes was identified as a specific response of sorghum to combined stress. Similar trends were observed for *Arabidopsis* [82], tobacco [83], and wheat [230]. Furthermore, *OsMYB55* is tolerant to high temperatures and drought stress in maize [231]. An analysis of OsMYB55 transgenic maize revealed the significant upregulation of genes associated with abiotic stresses, such as heat, dehydration, and oxidative stress [231]. This suggests that plants perceive combined stress as a unique transcriptional response during adaptation. Interestingly, drought and heat abiotic stresses induce several transcription factors, such as the ethylene-responsive transcriptional co-activator, dehydration-responsive element-binding proteins (DREBs), and WRKY, to improve plant endurance [82,83], calcium transporter ATPase 9, and proteins involved in disease resistance [232]. Some transcription factors that are well-known master regulators of stress-responsive genes under abiotic stresses (drought and heat) have been extensively studied because of their vital roles in crop yield improvement [233]. For example, a DREB2 transcription factor from sorghum, the *SbDREB2* gene, showed higher resistance to water deficit than the wild type in transgenic rice [234], and potato *StDREB* also showed the same resistance in transgenic cotton [235]. In *Arabidopsis* and wheat, AtDREB1A and TaDREB1A exhibit high tolerance to abiotic stress [236]. Furthermore, in barley, HD-zip genes (*HDZI-3* and *HDZI-4)* from wheat can be used in combination with DREB/CBF transcription factors to enhance abiotic stress (drought) tolerance and improve crop yield [237]. Increased levels of phytohormone ABA, which plays a key role in regulating several plant responses during abiotic stress, in dry soil helps in the maintenance of root growth, hydraulic conductivity, and water uptake [208]. ABA is also transported via the xylem to the shoot, inducing stomatal closure to reduce the water use efficiency [208]. As the transcriptome can vary depending on the type of plant, time, and severity of stress [228], the functions of proteins encoded by these genes and their associated metabolic pathways need to be further explored. This knowledge is crucial for a comprehensive understanding of the mechanisms involved in mitigating the combined effects of drought and heat stress. This understanding can be useful in arid and semi-arid regions such as Africa, tropical parts of India, and Latin America where crops such as *Sorghum bicolor* hold significant importance as grain crops [229]. These studies indicate the substantial advancements in the development of crop varieties well suited for agriculture in arid and semi-arid regions.

5. Conclusions

In this review, the multifaceted exploration of factors affecting global crop production revealed the critical challenges posed by environmental stresses, such as soil acidity, Al and Fe toxicity, drought, and heat stress. The far-reaching consequences of these factors on nutrient balance and crop yield, particularly in tropical regions, highlight the urgent need for new strategies to address these issues. The integration of organic and inorganic fertilizers with region-specific nutrient management practices has emerged as a key solution to enhance soil health and mitigate environmental stress. In SSA, ISFM is used as a strategic approach combining organic and inorganic fertilizers to improve nutrient efficiency. This article also discussed the beneficial effects of enhancing nitrogen and phosphorus uptake, mitigating drought and heat stress in semi-arid regions, and tailoring practices to different agroecological zones. The further exploration of Al tolerance mechanisms revealed the complex strategies used by plants. The identification of key players, such as the ALMT1 and MATE family members and STOP1 transcription factor, highlighted the potential of genetic factors to overcome Al stress and other growth-limiting processes. This review lays the foundation for the further investigation of STOP1-mediated stress tolerance and facilitates the development of crop varieties resilient to different environmental conditions. The interplay between drought and heat stress poses a substantial threat to global agriculture, particularly tropical crops. The adaptive complexity of plant responses, including escape, avoidance, and tolerance strategies, emphasizes the dynamic nature of the plant defense system. The shared defense mechanisms of various plant species present new avenues for targeted research and stress tolerance interventions. Transcriptomic analyses of various plants under combined drought and heat stress provide valuable insights into the specific gene expressions and pathways involved in stress mitigation, suggesting new targets for crop improvement. Continued research and innovative approaches are crucial to navigate the complex landscape of climate change and its impact on agriculture. This article reveals the ongoing efforts to develop sustainable strategies for food security to overcome the escalating abiotic stresses. The findings presented here may impact the agricultural practices used in various regions and aid in adapting crops to challenging environments and fostering sustainable agricultural practices.

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