horticulturae

Review

Understanding the Impacts of Crude Oil and its Induced Abiotic Stresses on Agrifood Production: A Review

Johnson Odukoya [1,2], **Ronnie Lambert** [1] and **Ruben Sakrabani** [1,*]

[1] School of Water, Energy and Environment, Cranfield University, Cranfield MK43 0AL, UK; joodukoya@futa.edu.ng (J.O.); rjwlambert@gmail.com (R.L.)
[2] Chemistry Department, The Federal University of Technology, PMB 704 Akure, Ondo State, Nigeria
* Correspondence: r.sakrabani@cranfield.ac.uk

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Abstract: In many parts of the world, the agricultural sector is faced with a number of challenges including those arising from abiotic environmental stresses which are the key factors responsible for most reductions in agrifood production. Crude oil contamination, an abiotic stress factor and a common environmental contaminant, at toxic levels has negative impacts on plants. Although various attempts have been made to demonstrate the impact of abiotic stresses on crops, the underlying factors responsible for the effects of crude oil and its induced abiotic stresses on the composition of the stressed plants are poorly understood. Hence, this review provides an in-depth examination of the: (1) effect of petroleum hydrocarbons on plants; (2) impact of abiotic environmental stresses on crop quality; (3) mechanistic link between crude oil stress and its induced abiotic stresses; as well as (4) mode of action/plant response mechanism to these induced stresses. The paper clearly reveals the implications of crude oil-induced abiotic stresses arising from the soil-root-plant route and from direct application on plant leaves.

Keywords: agrifood; crude oil contamination; crop quality; environmental stresses; petroleum hydrocarbons; stressed plants

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1. Introduction

Crude oil pollution, arising from exploration and processing operations, is a common environmental challenge [1]. This introduction of crude oil (via large or small spills) into the environment could arise from technical errors, deliberate human acts as well as transportation and storage faults [2–6]. Schmidt-Etkin [7] noted that although large spills sometimes occur with serious environmental and socioeconomic damage, small spills are more common. As explained in detail in a later section, the impacts and damages caused by these spills generally depend on the location, oil type, volume, closeness to sensitive resources, and season, among other factors [7]. Nonetheless, accidental large-scale oil spills make up a significant part of contaminants in the globe [8]. There are more cases of oil spills on land than those recorded in water [4] in which plant life in agricultural fields becomes exposed to petroleum hydrocarbons (PH) [8] with both acute and chronic effects on agricultural produce [1].

Interestingly, the various technological/prevention measures coupled with better industry practices have helped in the global reduction in oil spillage but the risk involved in significant oil spills remain [7]. Table 1 provides a record of the largest oil spill cases in the world's history.

Table 1. The top 20 largest oil spills (>125,000 tonnes) in world's history.

S/N	Location	Source Name	Quantity (Tonnes)	Date
1.	Kuwait	700 oil wells	71,428,571	10 March 1991
2.	Kuwait	Min al Ahmadi Terminal	857,143	20 January 1991
3.	Russia	Oil wells	700,000	3 August 2000
4.	United States	Deepwater Horizon	686,000	20 April 2010 *
5.	Mexico	Ixtoc I well	476,190	3 June 1979
6.	Iraq	Bahra oil fields	377,537	1 February 1991
7.	Uzbekistan	Oil well	299,320	2 March 1990
8.	Trinidad/Tobago	TN Atlantic Express	286,354	19 July 1979
9.	Russia	Kharyaga-Usink Pipeline	285,714	25 October 1994
10.	Iran	No. 3 Well (Nowruz)	272,109	4 February 1983
11.	South Africa	TN Castillo de Bellver	267,007	6 August 1983
12.	France	TN Amoco Cadiz	233,565	16 March 1978
13.	Canada	TN Odyssey	146,599	10 November 1988
14.	Italy	TN Haven	144,000	11 April 1991
15.	Libya	D-103 concession well	142,857	1 August 1980
16.	Nigeria	Pipeline	142,857	6 January 2001
17.	Kuwait	TN Al Qadasiyah	139,690	19 January 1991
18.	Kuwait	TN Hileen	139,690	19 January 1991
19.	United Kingdom	TN Torrey Canyon	129,857	18 March 1967
20.	Oman	TN Sea Star	128,891	19 December 1972

* From Ivshina et al. [4] as well as Levy and Gopalakrishnan [9]; others adapted from Schmidt-Etkin [7].

Although the effect of PH such as from crude oil spills in the environment has been studied for many years, even with respect to the impact on plants, there is still a gap in understanding how the composition of the affected plants is influenced. Some researchers, such as Levy and Gopalakrishnan [9], Okpokwasili and Odokuma [10], Njoku et al. [11], and Ylitalo et al. [12], have reported the effect of crude oil spills on the general environment while others like Venosa et al. [13], Ebuehi et al. [14], Couto et al. [15], as well as Adekunle [16], have indicated how the remediation of such polluted sites can be carried out. Various remediation approaches, including bioremediation, have been suggested.

Evaluation of the effect of crude oil on plant growth/yield has also gained attention and the outcome of such investigations have been documented in Kuhn et al. [17], Adam and Duncan [18], Adieze et al. [19], Inckot et al. [20], Baruah et al. [21], as well as Odukoya et al. [22,23]. Nonetheless, the effects of crude oil on the composition and quality of crops still remain unclear. In most cases, such as in Baruah et al. [21], Chupakhina and Maslennikov [24], and Noori et al. [25], the impact of crude oil on only a few crop quality parameters was investigated.

Considering the human dependence on agricultural produce for food, this review provides needed information on the impact of crude oil-induced abiotic stresses on plant composition. It discusses the general impact of abiotic environmental stresses on the composition of agricultural produce (particularly with respect to crop quality), and summarises the relationship between these stresses (i.e., crude oil stress and its induced abiotic stresses) via a mechanistic link to provide clarity on the response patterns observed in crude oil-stressed plants. A chemical classification of petroleum hydrocarbons is provided in Figure 1.

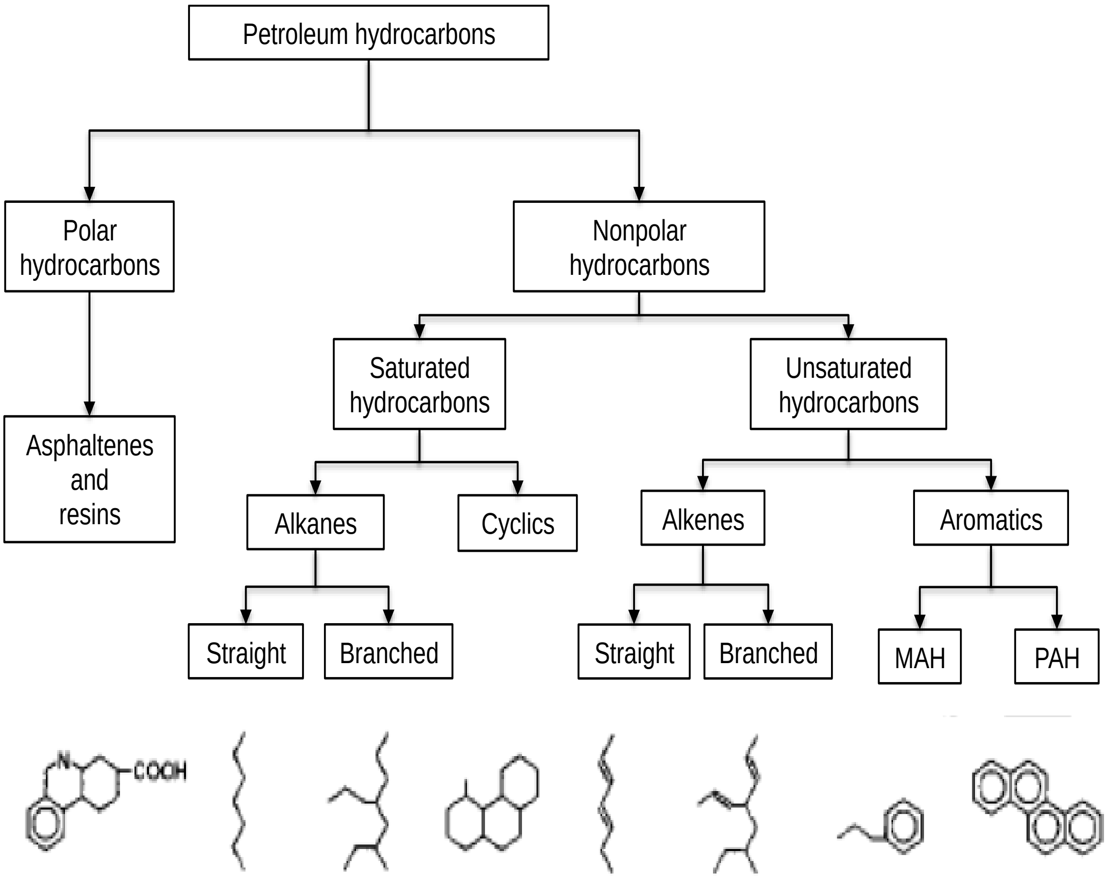

Figure 1. Chemical classification of petroleum hydrocarbons. (MAH = Monoaromatic hydrocarbons; PAH = Polycyclic aromatic hydrocarbons). Source: Coulon and Wu [26].

2. Effects of PH on the Growing Environment and Plants

The behaviour of PH in the environment determines where they are likely to be found, such as in air, water, soil, sediment, food, or other media that people might come in contact with [27]. In the view of Oghenejoboh et al. [28], the factors governing the spread/migration of spilled oil in soil include the amount of oil spilled, physical properties of the spilled oil (density and viscosity), and physical properties of the soil medium itself, particularly its porosity. Although the introduction of PH affects the physical, chemical, and biological properties of soil [7], these factors (i.e., the soil type, quantity, and composition of the spilled hydrocarbon) also determine the level of alteration of the soil properties [27,29].

On agricultural lands, Plice [30] and also De Jong [31], reported that oil spills can result in reduced plant growth for some time. PH contamination which is associated with an increase in carbon/nitrogen (C/N) ratio and nitrogen deficiency [32], may also lead to a reduction in plant stem height, stem density, aboveground biomass, and include death of the plant [33–37]. Meanwhile, the response of plants to the presence of PH in soil varies [20,38,39] and is associated with the plant age [40], species of the plant involved, type and concentration of the petroleum, time of exposure to the contaminant [20,29,38] as well as the season [36,41], among other factors.

De Jong [31], referring to the experiment of Carr [42], indicated the possibility of a low concentration of crude oil in the environment supporting plant growth. Although this test was conducted in duplicate, Carr [42] found out that at 0.75% *w*/*w* of crude oil addition to the soil, the growth of soybeans was improved. Adieze et al. [19] also recorded an increase in shoot height and weight of two of the plant species examined at 1% *w*/*w* oil-in-soil. This stimulating effect according to Plice [30] may be as a result of the bacterial breakdown of the hydrocarbons. Other possible reasons for plant growth-stimulation, as suggested by Baker [38], although subject to further investigation, could be attributed to the release of nutrients from the oil, oil-killed vegetation, or hormonal influence. Be that as it may, there are claims that this occurrence in plants is a result of 'petroleum auxin' identified as naphthenic acids, which (i) improve the yield of different varieties of crops; (ii) stimulates photosynthesis; and (iii) increases protein nitrogen [38].

Notwithstanding possible positive effects, most studies regarding the growth of plants in soil containing PH have reported negative effects [20] including on the germination of seeds [18,20]. Reductions in the plant growth could be a result of (1) the direct toxic effect of oil on plants [31,38]; (2) absence of viable seeds leading to lack of germination; (3) reduced germination; (4) unfavourable soil conditions [31]; and (5) inhibition of bacterial decomposition of the soil organic matter and associated nutrient remineralization by the toxic components of oil [40]. The inhibition of germination may be linked to oil entering the seed and killing the embryo, or oil coating the seed and hindering the uptake of oxygen and water required for germination [38]. Merkl et al. [32] added that reduced seedling emergence could be as a result of toxic effects of the oil or from the adverse soil moisture conditions. Other effects of oil pollution on plants as stated by Baker [38] include yellowing and death of oiled leaves, varying sensitivity, and recovery rates of perennials, among others, while a complete elimination may occur at chronic levels. Heavier oils compared to lighter oils present less immediate toxic impact on plants and other organisms [40].

Baker [38] indicated that photosynthetic rate is consistently reduced by oils, while the level of reduction in this rate depends on the kind and amount of oil as well as the plant species. For instance, the experiment of Odukoya [5] involving selected green leafy vegetables (GLV) and a fruit vegetable (tomato (*Solanum lycopersicum*) indicated that the effect of crude oil contamination on the species differed. Generally, crude oil at the concentration used in this experiment {≤10,000 mg/kg total petroleum hydrocarbons (TPH)} altered stomatal conductance (a measure of the rate of diffusion of carbon dioxide (CO_2) into leaves for photosynthesis, and water loss via transpiration [43]), growth, yield, and composition of the GLV. Figures 2 and 3 show the impact of the crude oil contamination on the stomatal conductance (mmol/m^2s) as well as growth of *Brassica juncea*, *Brassica oleracea*, and *Lactuca sativa*. The effect on the flower production date of *B. juncea* is also provided in Figure 4. The influence on yield and levels of phytochemicals in the selected GLV has been previously discussed (see Odukoya et al. [23]).

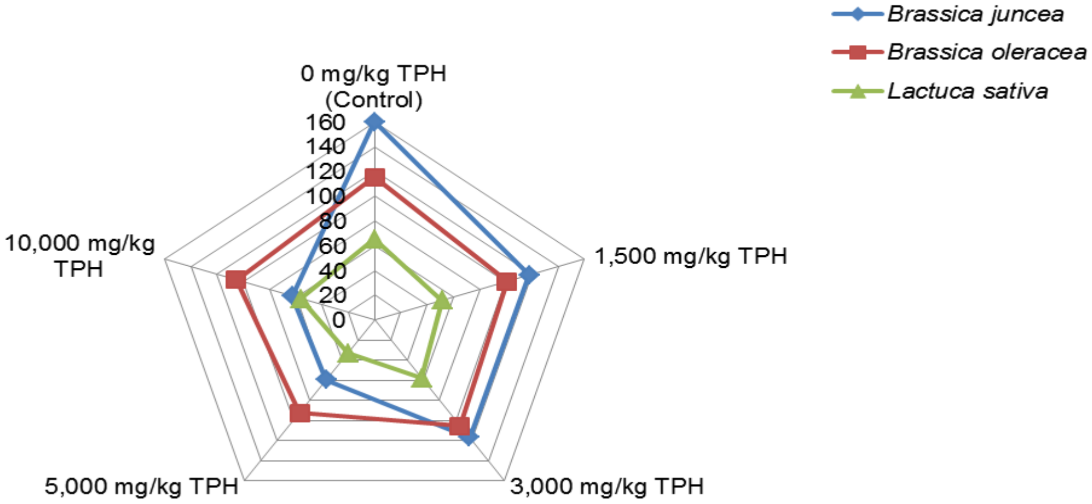

Figure 2. Effect of crude oil contamination on stomatal conductance (mmol/m^2s) of selected green leafy vegetables prior to harvest. Source: Odukoya [5].

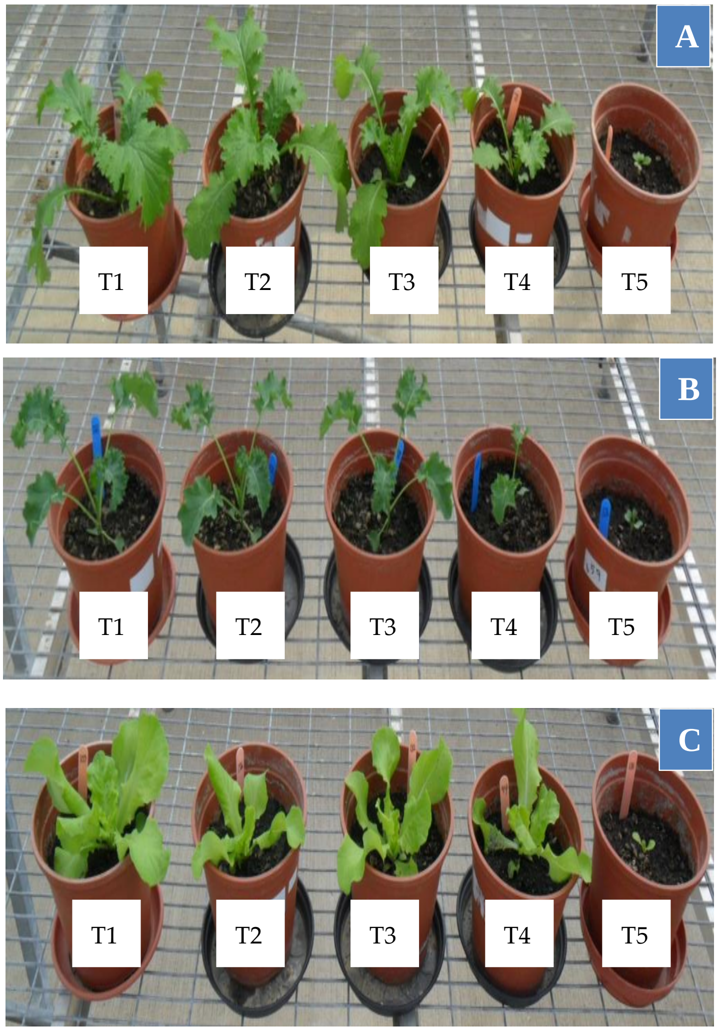

Figure 3. The growth of three green leafy vegetables ((**A**) *B. juncea*, (**B**) *B. oleracea* and (**C**) *L. sativa*) in pots containing crude oil at different concentrations. Treatments T1, T2, T3, T4 and T5 are 0 mg/kg TPH (Control), 1500 mg/kg TPH, 3000 mg/kg TPH, 5000 mg/kg TPH, and 10,000 mg/kg TPH, respectively. Source: Odukoya [5].

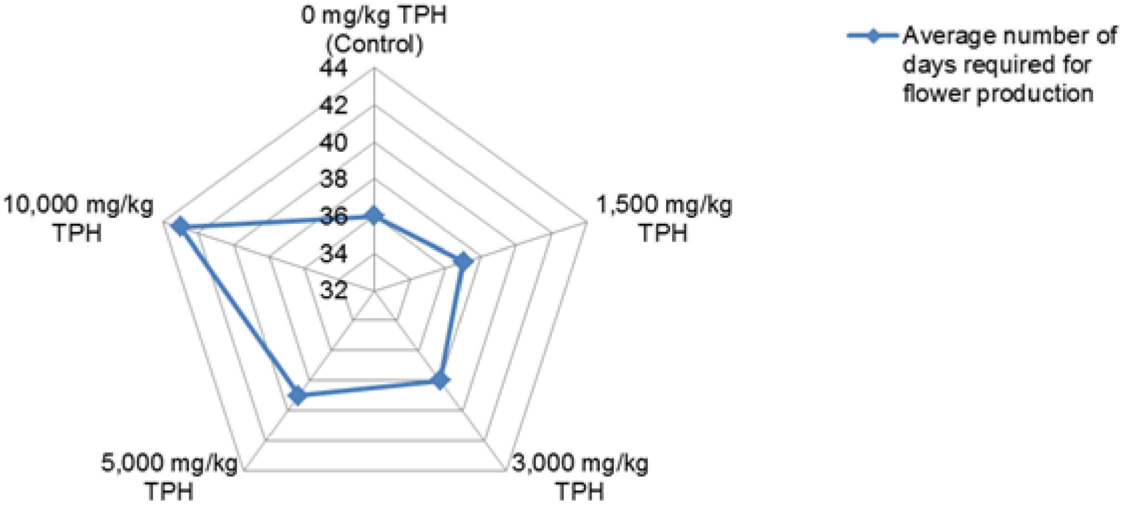

Figure 4. The effect of crude oil contamination on flower production date of *B. juncea*. Source: Odukoya [5].

Odukoya et al. [5,22] also recorded that crude oil contamination at concentration as low as 5000 mg/kg TPH affected the growth, yield, fruit production, and ripening of Micro-Tom tomato fruits (Figure 5).

Figure 5. Growth of Micro-Tom tomatoes in pots containing crude oil at 0 mg/kg TPH (left plant) and 5000 mg/kg TPH (right plant), before fruiting (**A**) and during ripening (**B**). Source: Odukoya [5].

Considering the effect of time of spillage on plant response, Baker [38] reported that application of an emulsion of light oil on young plants in the light when the stomata are opened will lead to death of the plant while the same application at night when the stomata are closed would not harm them. Baker [38] also indicated that there is an increased level of phytotoxic risk at high environmental temperature (such as during sunny or hot weather) compared to other times.

3. Abiotic Environmental Stresses and Crop Quality

Abiotic stresses, which include environmental contaminants [44], have been identified as the key factors responsible for most of the reduction in agrifood production (Figure 6); they also play a major role in determining the nutritional value/quality of fruits and vegetables during their growth, harvesting, handling, storage, and transport to end users [45]. The impact made by these abiotic stresses have been found to depend on the (1) the part (tissue or organ) of the plants involved [45,46]; (2) crop species; (3) duration; as well as (4) intensity of the stress [47] and could cause morphological, physiological, biochemical, and molecular alterations within the affected plants [45]. Retardation of plant growth may also occur as the plants make efforts to conserve and reallocate resources that can become limited under extreme stress conditions [48].

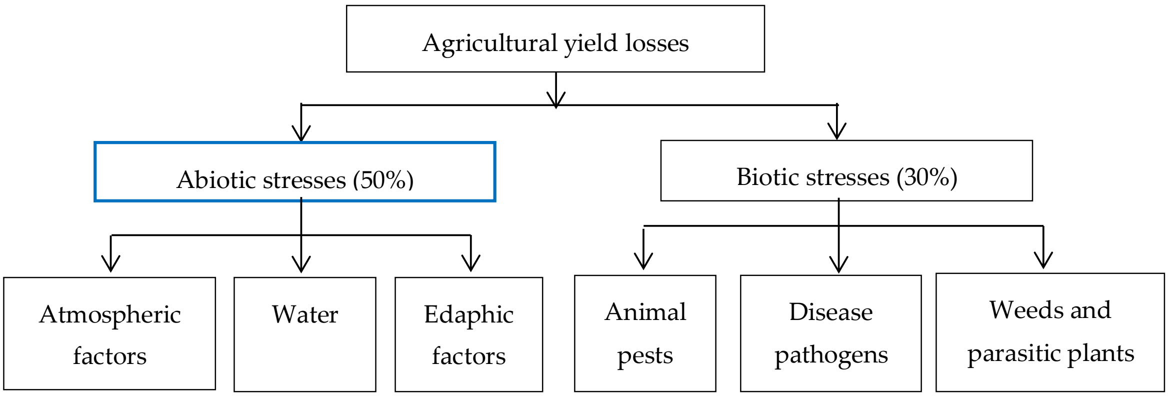

Figure 6. Agricultural yield losses due to abiotic and biotic stress. Adapted from: Gaur and Sharma [49].

Wang and Frei [47] indicated that all quality traits of agricultural produce can be influenced by abiotic environmental stress factors which can be linked with the different physiological reactions/responses in the affected plants as a result of changes in gene expression and enzyme activity, oxidative stress arising from the accumulation of reactive oxygen species (ROS), accelerated senescence, which shortens the crop maturity period and alters the nutrient distribution processes within the stressed plants, reduced water content which leads to increase in nutrient content, changes in mineral uptake and translocation, as well as reduced biomass/yield which is the most obvious and identified effect of abiotic environmental stress on agricultural produce. Although some crops respond differently, in most cases, environmental stresses cause (1) a decrease in starch concentration, lipids {particularly the polyunsaturated fatty acids (PUFA)}, feed value, and physical/sensory (P/S) traits; (2) an increase in protein and antioxidant contents; and (3) no clear trend in sugar and mineral contents [47].

On the other hand, one of the common mechanisms by which plants adapt to abiotic stresses encountered in the environment involves the accumulation of compatible solutes which are highly soluble and low molecular weight compounds with no toxic effect at high concentrations [50]. The different forms of these compounds accumulated may be species-specific and include amino acids (like proline), glycine betaine, sugars (such as sucrose, and trehalose), and sugar alcohols (like sorbitol and mannitol) [50–52]. These compatible solutes do not interfere with normal cellular metabolism [52,53].

4. Mechanistic Link between Crude Oil Contamination and Induced Abiotic Stresses

4.1. Induced Physical Influence

The coating of plant leaves with oil may lead to temperature stress owing to the blockage of the transpiration pathways while the process of photosynthesis in the leaves would be negatively affected [40,54]. The penetration of oxygen into the soil could also be restrained by the layer of oil covering the soil surface resulting in anaerobic soil conditions for the plant roots [20,40] and contributes to oxygen stress on these roots [40].

Nevertheless, the level of reduction in transpiration and photosynthesis arising from the physical blockage of the stomata depend on the extent of oil covering on the plant which is associated with the hydrologic conditions, amount, type, and dispersion ability of the spilled oil [40].

4.2. Induced Chemical Influence

The chemical impact of oils on vegetation depends on the type of oil while the fouling of leaves by oil may have more immediate effects than fouling of the soil surface [40]. Pezeshki et al. [40] reported that reduced stomatal conductance with no detectable photosynthetic activity was evident shortly after leaf fouling which suggests potential breakdown of the photosynthetic apparatus in the leaves directly subjected to oil application. In their view, this breakdown of leaf structure and/or the chlorophyll system may be associated with blocked stomata giving rise to reduced transpiration, thus increasing the leaf temperature with the possibility of an adverse effect of the oil on cellular integrity of the leaf tissue. They added that plants may recover from the initial, short-term (often dramatic) adverse effects of oil on leaves while refined products, compared to crude oils, present a different effect on leaves.

Furthermore, as plants like other organisms produce ROS in response to abiotic and biotic stresses [55], environmental contamination arising from PH reduce the availability of essential nutrients (like nitrogen and oxygen) required for plant growth [19,56], including water [57] owing to the surface covering of the plant roots by the hydrophobic contaminant, thereby enhancing the production of ROS and hence, oxidative stress in plants [55,58].

Basically, PH may affect plants by (1) upsetting the plant-water relationships; (2) direct effect on plant metabolism such as nutrient uptake [36]; (3) their toxicity to living cells [26,59]; and (4) the reduction in oxygen exchange between the atmosphere and the soil which have negative effects on plants [36,60].

4.3. The Mechanistic Link

Crude oil/PH contamination, an abiotic factor [61], leads to oxidative stress in plants [25] and gives rise to the production of ROS. Figure 7 shows the mechanistic link between crude oil contamination/stress and identified crude oil-induced abiotic stresses.

5. The Mode of Action/Plant Response Mechanisms to the Crude Oil-Induced Abiotic Stresses

5.1. Water (Drought) and Osmotic Stresses

"Drought is a meteorological term for a scarcity of water" ([62], p. 510) while water stress on plants occurs when there is a limitation of water supply to the roots, or when the transpiration rate exceeds the absorption rate [45,63]. Photosynthesis and growth are among the key processes affected by drought [64,65] whose effects can: (1) be direct, such as resulting from the alteration in the diffusion of CO_2 in leaves via a decrease in stomatal and mesophyll conductances [65,66]; or (2) give rise to secondary effects-oxidative stress [65]. In Farooq et al. [67], it was added that drought is also associated with accelerated leaf senescence and reduction in crop yield.

5.1.1. Plants' Responses to Water Stress

Akinci and Losel [68] indicated that plant adaptation to dry environments can be expressed at four different levels which are phenological or developmental, morphological, physiological, and metabolic while the latter (metabolic or biochemical adaptation) is the least understood. Whereas some responses of plants to water stress occur at the leaf level [69], it is the general response at the whole-plant level, involving carbon assimilation and the distribution of photoassimilates to different plant parts and reproductive ability that eventually determine the survival of these plants and persistence under environmental stress [69]. Nonetheless, carbon assimilation at this whole-plant level always decreases as a result of (1) reduction in CO_2 diffusion into the leaf; (2) diversion of carbon distribution to non-photosynthetic organs and defence molecules; or (3) biochemical changes in the leaf leading to the down-regulation of photosynthesis [69]. The various responses of plants to water stress are summarised in Table 2.

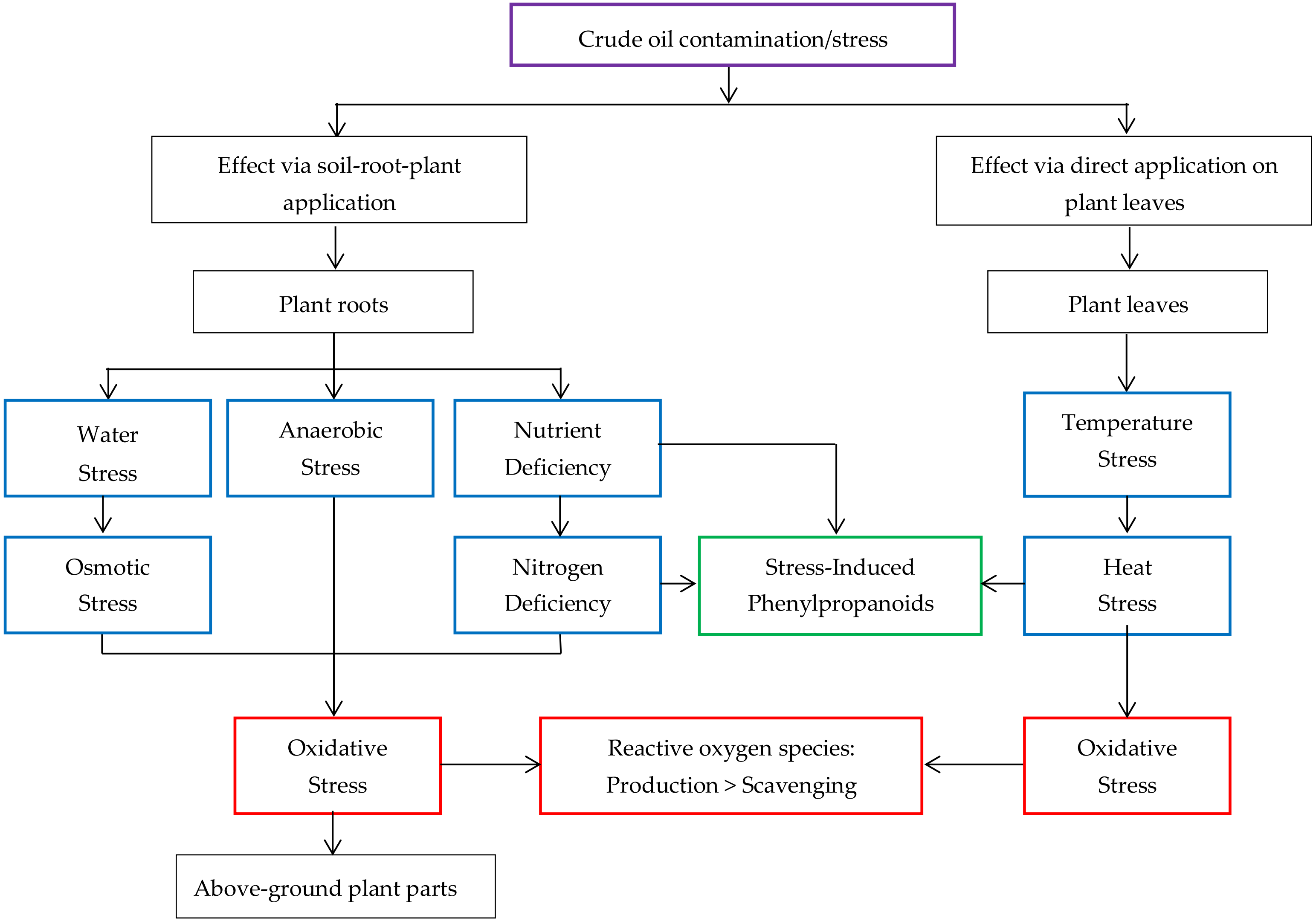

Figure 7. Illustration of the mechanistic link between crude oil contamination/stress and the crude oil-induced abiotic stresses as it affects agrifood production.

Table 2. Summary of plants' responses to water stress.

Type of Response	Impact Indicators	Parts of Plants/Processes Affected	References
Morphological and physiological responses	Crop growth and yield	Reduced growth parameters such as height, leaf number, leaf area index as well as fresh and dry weight.	Akinci and Losel [68] Timpa et al. [70]
		* Shoot growth may be more inhibited than root growth.	Sharp [71] Sharp and Davies [72]
	Water relations	Affects plant water relations, stomatal closure, gas exchange, transpiration, and carbon assimilation (photosynthesis).	Lisar [63]
		* Stomatal opening and closing is more strongly influenced.	Farooq et al. [67]
	Nutrient relations	Reduced ability of plant roots to absorb water and nutrients which could be as a result of a decrease in nutrient element demand.	Akinci and Losel [68] Alam [73]
		Reduced availability, uptake, translocation and metabolism of nutrients.	Farooq et al. [67]
		Increase in K, Na, Ca, Mg, and Cl; decrease in P and Fe.	Abdel Rahman et al. [74]
		Increase in N; decrease in P; no effect on K.	Farooq et al. [67]
	Osmotic adjustment	Lowering water deficiency impact and linked to the maintenance of stomatal conductance, photosynthesis, leaf water volume, and growth.	Akinci and Losel [68]
		* Most often temporary as plants usually respond quickly to increase in the level of available water.	
		* Solutes accumulate with water stress and contribute to osmotic adjustment in non-halophytes including inorganic cations, organic acids, carbohydrates, and amino acids.	
	Photosynthesis	Negative effect on photosynthesis of crops and possibly a cessation in the photosynthetic process.	Akinci and Losel [68]
	Assimilate partitioning	Often enhanced allocation of dry matter to the roots increasing root growth which can support greater water uptake.	Farooq et al. [67]

Table 2. *Cont.*

Type of Response	Impact Indicators	Parts of Plants/Processes Affected	References
Metabolic and molecular responses	Carbohydrate changes	For moderate water stress, plant response is more regulatory rather than stress-induced damage.	Chaves [64]
		Accumulation of sugars and other organic solutes.	Akinci and Losel [68]
	Plant proteins	Reduction in plant protein synthesis.	Akinci and Losel [68] Dhindsa and Cleland [75] Ben-Zioni et al. [76]
		Levels of some specific types of proteins and mRNA may increase.	Akinci and Losel [68]
		* Three kinds of osmolytes found in water stressed organisms except the halobacteria include polyhydric alcohols, free amino acids, and their derivatives, combinations of urea and methylamines.	Yancey et al. [77]
	Plant lipids	Contradictory reports on the effect on plant lipids.	Akinci and Losel [68]
		Hindered fatty acid desaturation which gives rise to a sharp decrease in linoleic and linolenic acid biosynthesis.	Akinci and Losel [68] Pham Thi et al. [78]
	Oxidative damage	Can lead to the production of ROS.	Teotia and Singh [79]

* Additional information.

5.1.2. Osmotic Stress

In line with Zhu et al. [80], osmotic stress may be used to refer to conditions in which there is a limitation on plant growth and development as a result of shortage of water availability. Although osmotic stress can result from drought, excessive salt in water, chilling, and freezing [80], Xiong and Zhu [81] identified drought and high salinity as the chief causes of stress to plants under natural conditions.

Plants respond to osmotic stress at the morphological, anatomical, and cellular levels [80] which results in alterations in their development (such as the plant life cycle, limitation of shoot growth, and enhancement of root growth), regulation in ion transport as well as metabolic changes which may involve carbon metabolism and production of compatible solutes [45,81]. Some of these responses according to Xiong and Zhu [81] are triggered by the primary osmotic stress signals while others can be linked to secondary stresses/signals resulting from the primary signals. Examples of the secondary signals are phytohormones [such as abscisic acid (ABA) and ethylene], ROS as well as intracellular second messengers (e.g., phospholipids) [81].

Generally, the response of plants to osmotic stresses can be classified into three different forms involving (a) the maintenance of homeostasis; (b) detoxification of harmful elements; and (c) efforts towards growth recovery [81].

5.2. Anaerobic Stress

Higher plants, being aerobes, need molecular oxygen from their environment for survival [82]. However, under certain environmental conditions, there is a possibility of shortage in the supply of O_2 to plant tissues [83]. When this happens, that is, when there is restricted aeration of part or all of the plant, "the resulting tissue hypoxia or anoxia inevitably suppresses oxygen-dependent pathways especially the energy-generating system, disturbs functional relationships between organs such as roots and shoots, as well as suppresses both carbon assimilation and photosynthate utilization" [82].

This shortage in the supply of oxygen has more direct effect on underground organs such as the roots and seeds; the shoot systems are then indirectly affected as a result of the negative impact of the stress on the root functions upon which the shoots depend [82]. The mitochondria have also been identified by Vartapetian et al. [84] as suffering from oxygen deficiency before other cell organelles are affected. Most plants tissues can, however, withstand anoxia (lack of oxygen) only for a short period of time before irreversible damage occurs [85].

Plants' Responses to Anaerobic Stress

Depletion of oxygen affects cell physiology; it alters gene expression, energy consumption, cellular metabolism, growth, and development [86]. Based on findings by the authors, Blokhina et al. [87] indicated that lack of oxygen primarily results in a decrease in adenylate energy charge, cytoplasmic acidification, anaerobic fermentation, increase in cytosolic Ca^{2+} concentration, alterations in the redox state, and a decline in the membrane barrier function. Low-oxygen (hypoxia) stress is also reported to induce significant changes in the transcriptome as well as a shift from aerobic to anaerobic respiration [88].

(a) Pasteur effect: Mustroph et al. [89] identified the Pasteur effect as a common eukaryotic response to oxygen deficiency at the cellular level. According to Winkler et al. ([90], p. 721), this definition "that the rate of fermentation rises when oxygen is excluded" for the Pasteur effect by Krebs [91] has long been accepted in place of that involving "the inhibition of glycolysis by respiration". Kennedy et al. [85] added that most anaerobic-intolerant plants exhibit a pronounced Pasteur effect.

(b) ROS production and oxidative stress: Like many other stress conditions, hypoxia is associated with the excess generation of ROS [87]. Along these lines, there are two models which suggest (1) a decrease in ROS under oxygen deprivation {low NADPH-nicotine adenine dinucleotide phosphate [92]—oxidase activity}; or (2) an increase in ROS due to inhibition of the mitochondrial electron transport chain.

(c) Gene expression: As the synthesis of several proteins involved in glycolysis and fermentation processes is induced in plants under anaerobic conditions [93], Agarwal and Grover [94] noted that plants respond to low O_2-stress condition via specific alterations in gene expression. Generally, anaerobiosis gives rise to the alteration of gene expression in plants which leads to the accumulation of anaerobic proteins (ANPs) [95] many of which are metabolic pathway enzymes [94].

5.3. Nutrient Deficiency

Plants need nutrient elements for their normal growth and development in which the deficiency in any required element will have a significant impact [96]. Clarkson et al. [97] indicated that the level of availability of certain mineral nutrients can alter plant transpiration, stomatal conductance, and root hydraulic conductivity while the deficiency of any of these three plant nutrients—nitrate, phosphate, and sulphate—in the growth medium, would impact the stomatal conductance and root hydraulic conductivity in a similar way.

In line with Kandlbinder et al. [98], there are two contrasting developmental and metabolic effects that can be induced by nutrient deficiency. At the first instance, which shows the adaptive response, the growth of plants may decrease in an organised manner in which the number as well as size of each part of the plant (involving the roots, leaves, shoots, and regenerative organs) are reduced while the metabolic activity and ‘fitness’ are to a large extent unaffected [98]. In the second, the unbalanced response gives rise to a disturbed environment and dysfunction of the whole plant—the plant becomes stressed [98].

5.3.1. Plants’ Responses to Nutrient Deficiency

(a) Biosynthesis of stress-induced phenylpropanoids: Environmental (biotic and abiotic) stresses like pathogen attack, wounding, nutrient deficiencies, and temperature, among others (Figure 8), are capable of enhancing the levels of phenylpropanoids in plants [99,100].

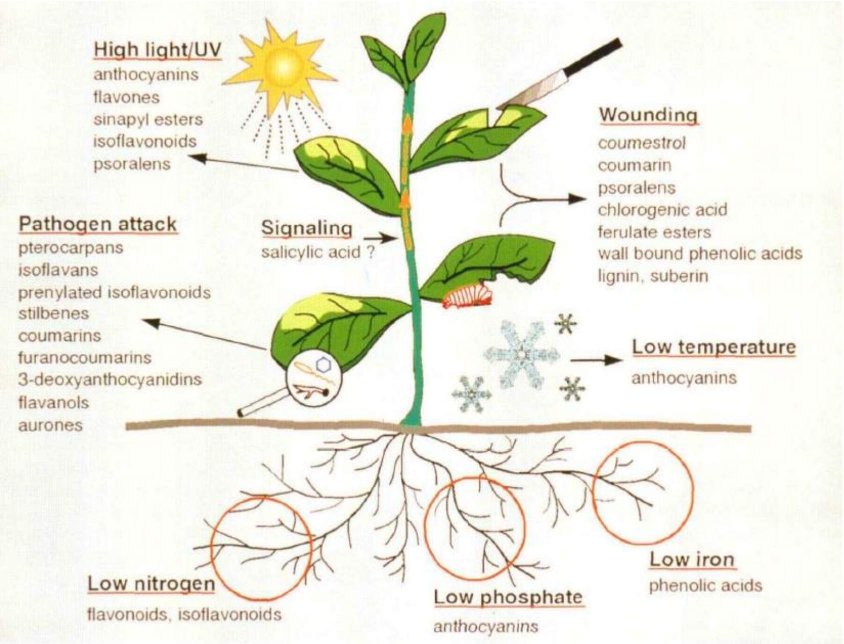

Figure 8. Examples of stress-induced phenylpropanoids. Source: Dixon and Paiva [100].

These phenylpropanoids are plant secondary metabolites [99,101,102] derived from *trans*-cinnamic acid, produced from the deamination of L-phenylalanine via the action of the enzyme—phenylalanine ammonia-lyase (PAL) [99,100]. The other two enzymes involved in the first three steps that brings about the synthesis of these secondary metabolites (phenylpropanoid-derived compounds), which together are referred to as the general phenylpropanoid pathway (GPP) (Figure 9), are cinnamate 4-hydroxylase (C4H) and *p*-coumaroyl coenzyme A ligase (4CL) [101].

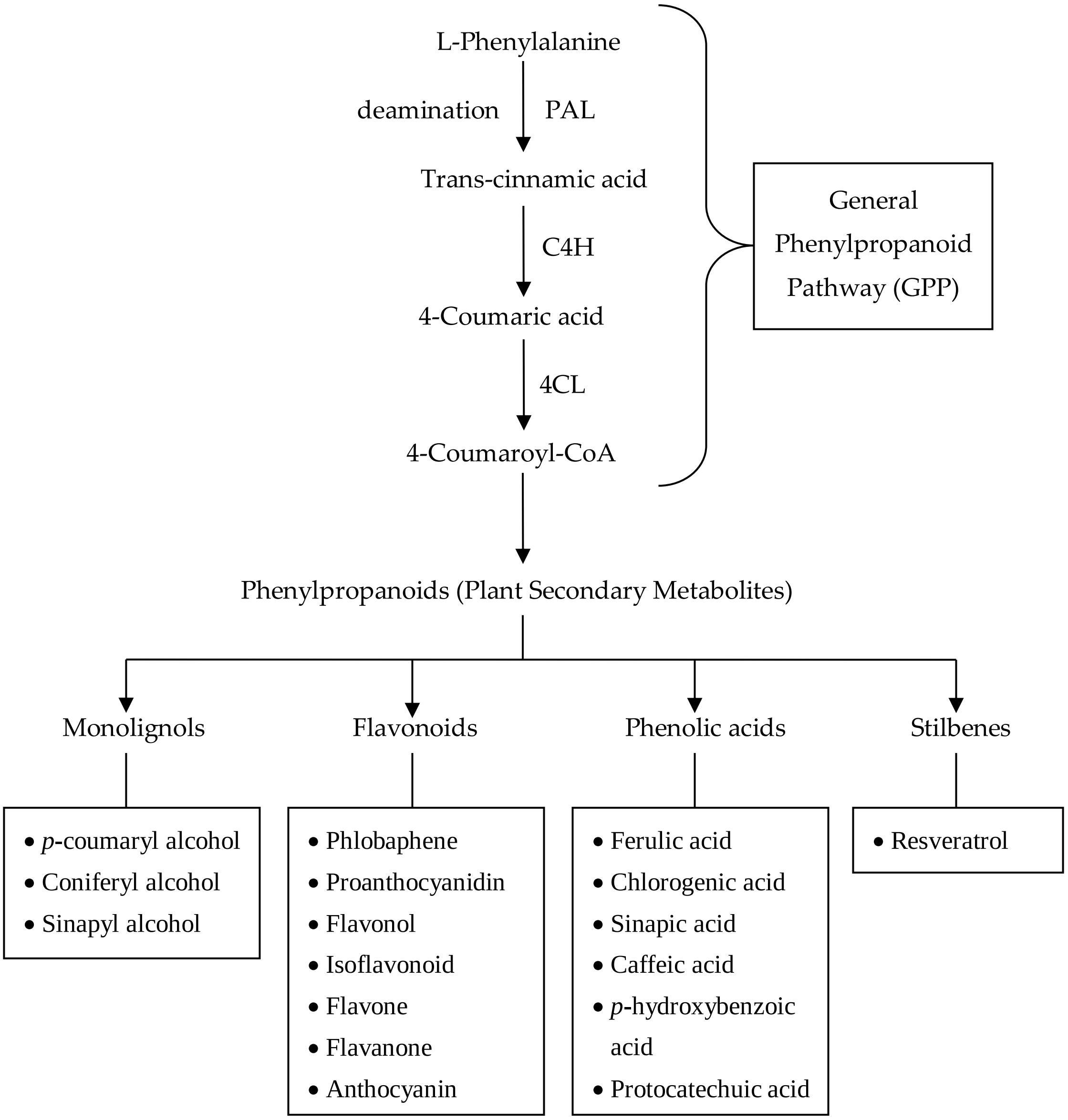

Figure 9. Biosynthesis pathway of some plant phenylpropanoid compounds (PAL = phenylalanine ammonia lyase; C4H = cinnamate 4-hydroxylase; 4CL = *p*-coumaroyl coenzyme A ligase). Adapted from: [101,102].

In line with Lillo et al. [103], the shikimate pathway is found in plants and provides phenylalanine for the synthesis of protein and secondary metabolites (like lignin and flavonoids). This shikimate pathway, with distinct patterns of organ-specific as well as tissue-specific activity, however, depends on developmental regulation and environmental stimuli [104]. The enzymes of this pathway also respond to nitrogen and amino acid starvation [104].

On the other hand, Gershenzon [105] indicated that nitrogen, phosphorus, potassium, and sulphur deficiencies most times lead to higher concentrations of phenolic compounds.

(b) Oxidative stress: Following the acknowledgment of the relationship between macronutrient deficiency and oxidative stress by Tewari et al. [106], Kandlbinder et al. [98] in their study found that N-, P-, and S-nutrient deprivation triggered redox changes and induced oxidative stress.

5.3.2. Nitrogen Deficiency/Stress

Aside from oxygen, carbon, and hydrogen, among other mineral nutrients, plants need greater amounts of nitrogen [107] whose deficiency Kovacik et al. [108] regarded as an abiotic stress factor based on the experimental results of Shin et al. [109] in which H_2O_2 production occurred in nitrogen-deprived roots. Kovacik et al. [110] also considered its absence as a form of abiotic stress.

Nitrogen deficiency is associated with increased phenolic concentration [105,108,111] including flavonoids [108,112,113] and coumarins [108,110]. It is, however, linked with reduced mass-based protein content [114]. In the view of Bongue-Bartelsman and Phillips [112], the increased deamination of phenylalanine could be responsible for elevated flavonoid content under nitrogen limitation.

In addition, Kovacik et al. [110] indicated that nitrogen deficiency will affect amino acids and carbon metabolism while Kovacik et al. [108] as well as Shin et al. [109] added that nitrogen limitation can encourage the generation of ROS. When the level of these ROS produced exceeds that of removal by the antioxidant defense mechanisms, oxidative stress occurs in the cell [115].

The indicators of senescence, which is an important outcome of N or P deficiency [106], is reported to be similar to those of oxidative stress which include net loss of chloroplastic pigments and proteins [106,116–118], lipid peroxidation, and membrane alterations, giving rise to a progressive decline in photosynthetic capacity [106,118].

5.4. Temperature (Heat) Stress

Although living organisms recognise temperature beyond the normal optimal as heat stress [119], Wahid et al. [120] referred the transient increase in temperature, usually 10–15 °C above ambient, as heat shock or heat stress. They also added that heat stress occurs when there is an increase in temperature above a threshold level for a period of time which can cause irreversible damage to plant growth as well as development. In other words, heat stress depends on the intensity (in terms of temperature in degrees), time of exposure, and rate of increase in temperature. For instance, very high temperatures may lead to severe cellular injury and cell death within minutes as a result of the damaging effect on cellular organization. However, at moderately high temperature, injuries, or death may still occur but after a long-term exposure [120].

Plants' Responses to Temperature (Heat) Stress

The direct adverse effects of high temperature include protein denaturation and aggregation, as well as increased fluidity of membrane lipids. Meanwhile, enzyme inactivation in chloroplast and mitochondria, inhibition of protein synthesis, protein degradation, and loss of membrane integrity are associated with indirect or slower heat injuries. The resultant effects of these injuries are starvation, growth inhibition, reduced ion flux as well as production of toxic compounds and ROS (Wahid et al. [120]). The established responses of plants to temperature/heat stress are highlighted in Table 3.

Table 3. Summary of plants' responses to temperature/heat stress.

Type of Response	Impact Indicators	Parts of Plants/Processes Affected	References
Morpho-anatomical and phenological responses	Morphological symptoms	High temperature leads to loss in yield.	Wahid et al. [120] Hasanuzzaman et al. [121] Guilioni et al. [122]
		High temperatures affect performance and crop quality characteristics.	Hasanuzzaman et al. [121]
	Anatomical changes	High temperature impacts anatomical structures at the tissue, cellular and sub-cellular levels in which the associated alterations may give rise to poor plant growth and productivity.	Wahid et al. [120]
	Phenological changes	Heat stress to some extent affects all plant vegetative and reproductive stages.	Wahid et al. [120]
		* The extent of possible damage depends on the developmental stage of the plant.	Wollenweber et al. [123]
Physiological responses	Water relations	When water is limiting, plant tissue water status is affected at high temperature.	Wahid et al. [120]
		Under field conditions, high temperature stress reduces water availability which negatively affects plant productivity.	Simoes-Araujo et al. [124]
	Accumulation of compatible osmolytes	This is a basic adaptive mechanism.	Wahid et al. [120] Bohnert et al. [125] Hare et al. [126] Sakamoto and Murata [127]
	Photosynthesis	At moderate heat stress, inhibition of photosynthesis is reversible. Severe heat stress causes permanent damage to the photosynthetic apparatus.	Salvucci and Crafts-Brandner [128]
		Has more significant effect on the photosynthetic capacity of C_3 plants than that of C_4 plants.	Wahid et al. [120]
		* Regarded as the physiological process most susceptible to high temperatures.	Wahid et al. [120]

Table 3. *Cont.*

Type of Response	Impact Indicators	Parts of Plants/Processes Affected	References
Physiological responses	Assimilate partitioning	Low to moderate heat stress may cause a reduction in source and sink activities giving rise to severe reductions in plant growth, economic yield, and harvest index. High temperatures affect the transport and transfer processes in plants because of assimilate partitioning taking place via apoplastic and symplastic pathways.	Wahid et al. [120]
	Cell membrane thermostability	Increases the kinetic energy and movement of molecules across membranes resulting in loosening of the chemical bonds within molecules in biological membranes.	Wahid et al. [120]
		Affects the tertiary and quaternary structures of membrane proteins.	
	Hormonal changes	Affects hormonal homeostasis, stability, content, biosynthesis, and compartmentalization.	Wahid et al. [120]
		Gives rise to increased levels of abscisic acid (ABA) which brings about modification of gene expression in response to stress.	
	Secondary metabolites	Induces production of phenolic compounds such as flavonoids and phenylpropanoids.	Wahid et al. [120]
Molecular responses	Oxidative stress	Increases production of ROS.	Hasanuzzaman et al. [129,130]
	Stress proteins	Leads to the expression of stress proteins as an adaptive mechanism.	Wahid et al. [120]

* Additional information.

5.5. Oxidative Stress

Oxidative stress is defined as a "state in which oxidation exceeds the antioxidant systems in the body secondary to a loss of balance between them" ([131], p. 271) and according to Lushchak ([132], p. 176) "its development is either the reason, or common event of many pathological states, including aging". In line with Lushchak [132], oxidative stress occurs in situations where the equilibrium between ROS generation and elimination is upset leading to their enhanced steady-state level. Birben et al. [92] referred it to a shift in balance between oxidant/antioxidant which favours the oxidants as shown in Figure 10. This perturbation of the equilibrium between generation and scavenging of ROS may be caused by various biotic and abiotic stress factors which are known to reduce global crop production [133].

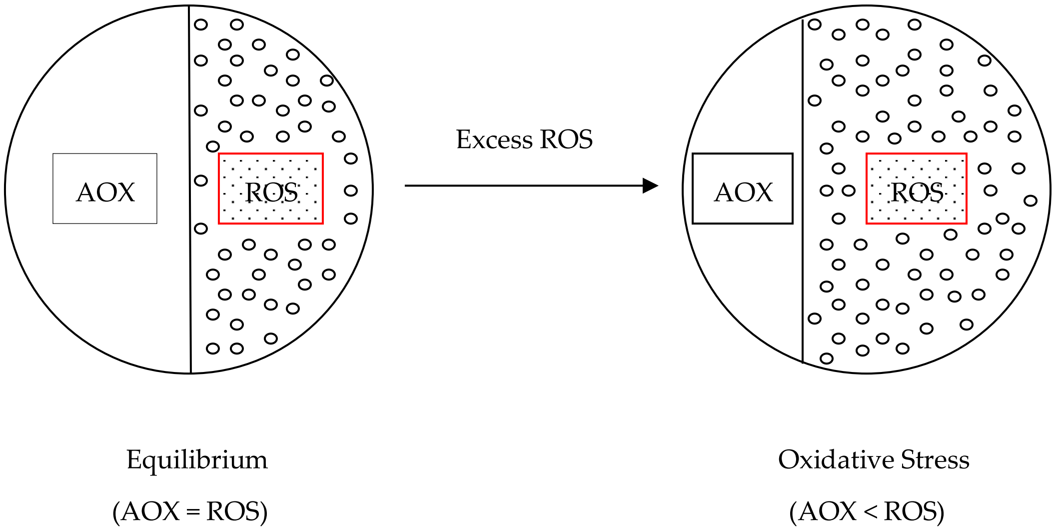

Figure 10. Relationship between oxidants (ROS) and antioxidants (AOX) leading to oxidative stress.

The ROS consists of free radicals, reactive molecules, as well as ions that are derived from O_2, which in plants, depending on their concentrations, can either be harmful or beneficial [115]. The most common ROS are singlet oxygen ($^1O_2$), superoxide anion ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical ($OH^{\bullet}$) [115]. At elevated concentrations, ROS bring about damage to biomolecules while at low/moderate concentration, they function as second messengers in intracellular signaling cascades that mediate several responses in plant cells [115] such as stomatal closure [115,134,135], programmed cell death [115,136,137], gravitropism [115,138], and acquisition of tolerance to both biotic and abiotic stresses [115]. Mittler [139] added that ROS levels that are too low (cytostatic level) or too high (cytotoxic level) have a negative effect on plant growth and development while ROS level within the right range (basal level) support plant health.

As noted by Sharma et al. [115], in plants, ROS are generated in both unstressed and stressed cells at different locations in chloroplasts, mitochondria, plasma membranes, peroxisomes, apoplast, endoplasmic reticulum, and cell walls. These authors added that the ROS are usually produced as a result of the leakage of electrons onto O_2 from the electron transport activities of chloroplasts, mitochondria, and plasma membranes or as byproducts of various metabolic pathways in different cellular compartments.

Generally, under ideal growth conditions, the generation of ROS in organelles is low [140] but are formed excessively during adverse/stressful conditions [140,141], which can bring about damage to biomolecules like lipids, proteins, and deoxyribonucleic acid (DNA) [115]. These reactions according to Sharma et al. [115] can affect intrinsic membrane properties such as fluidity, ion transport, loss of enzyme activity, protein cross-linking, inhibition of protein synthesis, and DNA damage, which eventually lead to cell death. Gill and Tuteja [142] pointed out that in addition to the ability of ROS to damage cells, they can also initiate responses such as new gene expression.

Plants' Responses to ROS and Oxidative Stress (Antioxidant Systems)

In line with Gill and Tuteja [142], the balance between generation of ROS and scavenging at the proper site as well as time, determines whether ROS will act as damaging, protective or signaling factors. Hence, as a result of the multifunctional roles of these ROS, cells must control their levels to prevent any oxidative injury but not eliminate them completely [115]. The scavenging or detoxification of excess ROS is carried out by the antioxidant system comprising the non-enzymatic antioxidants and enzymatic antioxidants [115]. The former class of non-enzymatic antioxidants within cells is comprised of ascorbic acid (AA), glutathione (GSH), carotenoids, α-tocopherol, phenolics and amino acids like proline while the latter class (enzymatic antioxidants) include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), and guaiacol peroxidase (GPX) [115,143].

Basically, the ability of plants to maintain a high antioxidant capacity to scavenge toxic ROS (i.e., reduce oxidative stress) implies increased plant tolerance level to environmental stresses [115,144]. Figure 11 provides a connection between the impact of the various levels of ROS on plants and the antioxidant system.

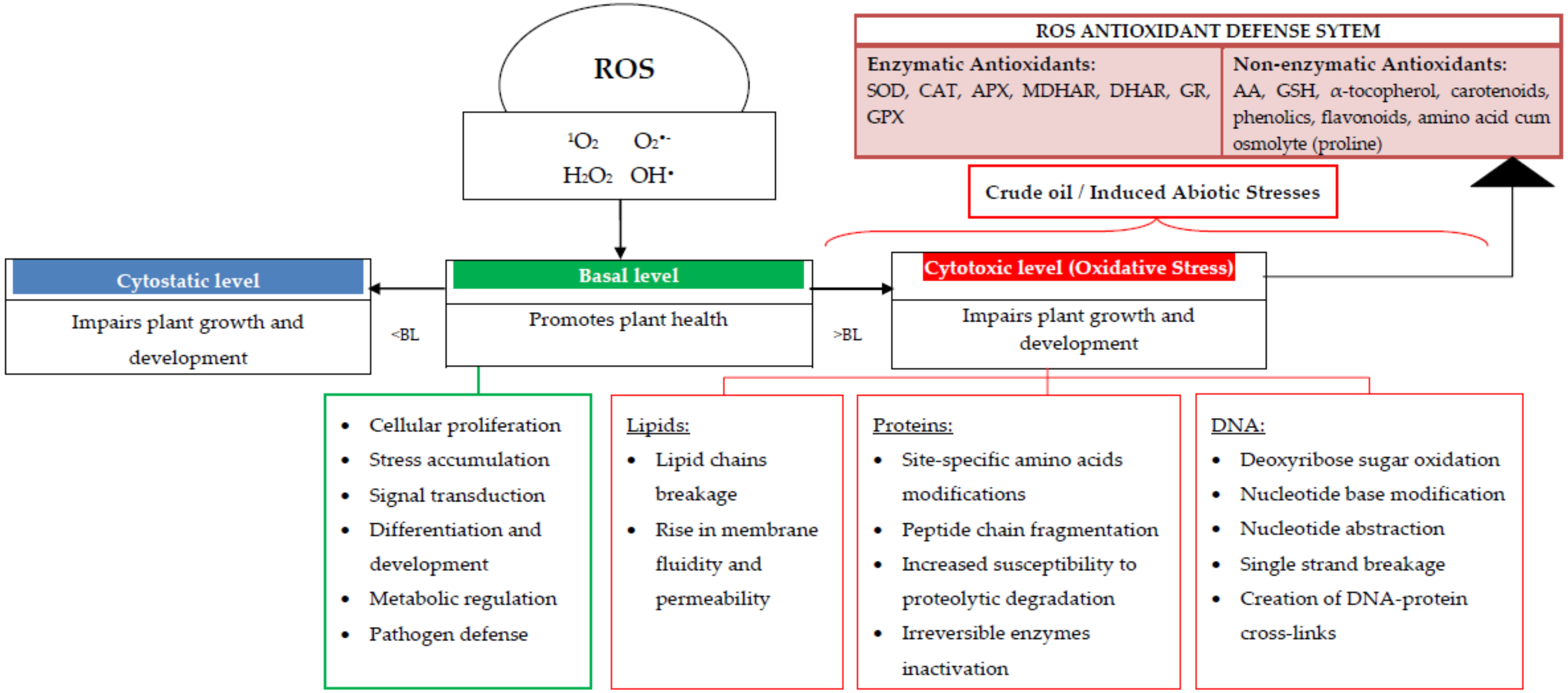

Figure 11. Connection between the impact of the various levels of ROS on plants and the antioxidant system. ROS = reactive oxygen species; BL = basal level; DNA = deoxyribonucleic acid; SOD = superoxide dismutase, CAT = catalase, APX = ascorbate peroxidase, MDHAR = monodehydroascorbate reductase, DHAR = dehydroascorbate reductase, GR = glutathione reductase, GPX = guaiacol peroxidase; AA = ascorbic acid, GSH = glutathione. Adapted from: Reference [115,139,142].

6. Conclusions

Although a number of studies have recorded the negative impacts of crude oil contamination at toxic levels on plants, this review elucidates the underlying factors responsible for the observed responses in the crude oil-stressed plants. It highlights the various ways in which crude oil and its induced abiotic stresses may affect the composition of agricultural produce. It is believed that a clear understanding on the influence of crude oil contamination/induced abiotic stresses on crop yield, quality, and agrifood production, in general, would assist the government, agronomists, environmental as well as food scientists in proffering solutions to the problem of food security in regions of the world prone to/affected by crude oil spills.

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