Growth regulators promote soybean productivity: a review

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Soybean [*Glycine max* (L.) Merrill] is a predominant edible plant and a major supply of plant protein worldwide. Global demand for soybean keeps increasing as its seeds provide essential proteins, oil, and nutraceuticals. In a quest to meet heightened demands for soybean, it has become essential to introduce agro-technical methods that promote adaptability to complex environments, improve soybean resistance to abiotic stress , and increase productivity. Plant growth regulators are mainly exploited to achieve this due to their crucial roles in plant growth and development. Increasing research suggests the influence of plant growth regulators on soybean growth and development, yield, quality, and abiotic stress responses. In an attempt to expatiate on the topic, current knowledge, and possible applications of plant growth regulators that improve growth and yield have been reviewed and discussed. Notably, the application of plant growth regulators in their appropriate concentrations at suitable growth periods relieves abiotic stress which increases the yield and yield components of soybean. Moreover, the regulation effects of the different growth regulators on the morphology, physiology, and yield quality of soybean are discoursed in detail.

1 **Growth Regulators Promote Soybean Productivity: A Review**

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20 INDEX

58 **Abbreviations**

59 PGRs: Plant growth regulators, IAA: Indole acetic acid, ABA: Abscisic acid, GA: Gibberellins,

60 ETP: Ethephon, JA: Jasmonic acid, DTA-6: diethyl aminoethyl hexanoate, Rubisco: Ribulose-1,

61 5 bisphosphate carboxylase, MBTA: diethyl-2-(4-methylbenzoxy) ethylamine, ROS: Reactive

62 oxygen species, GST: Glutathione S-transferase, NAA: Naphthalene acetic acid, DCPTA: 2-(3,4-

63 dichlorophenoxy) trimethylamine, GSH: Glutathione, ET: Ethylene, SA: Salicylic acid, CCC:

64 Chlormequat-chloride/2-chloroethyltrimethylammonium chloride, TIBA: Tri-iodo benzoic acid,

65 BMVE: 2-(N-methylbenzylaminoethyl)-3-methylbutanoate, BA: Benzyladenine, Kn: Kinetin,

66 BL: Brassinolide, BAP: 6-Benzylaminopurine, PEPCase: Phosphoenolpyruvate carboxylase,

67 RSA: Root surface area, IBA: Indole butyric acid, EBL: 24-epibrassinolide, GR: Glutathione

68 reductase, and WUE: Water use efficiency.

80   **Abstract**

81   Soybean [*Glycine max* (L.) Merrill] is a predominant edible plant and a major supply of plant

82   protein worldwide. Global demand for soybean keeps increasing as its seeds provide essential

83   proteins, oil, and nutraceuticals. In a quest to meet heightened demands for soybean, it has

84   become essential to introduce agro-technical methods that promote adaptability to complex

85   environments, improve soybean resistance to abiotic stress, and increase productivity. Plant

86   growth regulators are mainly exploited to achieve this due to their crucial roles in plant growth

87   and development. Increasing research suggests the influence of plant growth regulators on

88   soybean growth and development, yield, quality, and abiotic stress responses. In an attempt to

89   expatiate on the topic, current knowledge, and possible applications of plant growth regulators

90   that improve growth and yield have been reviewed and discussed. Notably, the application of

91   plant growth regulators in their appropriate concentrations at suitable growth periods relieves

92   abiotic stress which increases the yield and yield components of soybean. Moreover, the

93   regulation effects of the different growth regulators on the morphology, physiology, and yield

94   quality of soybean are discoursed in detail.

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1.0 Introduction

100

101 Grain legumes are vital and dominant group of crops after cereals such as wheat, rice, and maize

102 which contribute immensely to human nutrition. Their nutritive value is appreciable especially to

103 the developing world as these regions have inadequate supply of food derived from animal

104 sources (Shakya, Patel & Singh 2016). Among the legumes, soybean (*Glycine max* (L.) Merrill),

105 is a unique and distinct crop belonging to the *Fabaceae* (*Leguminosae*) family, order *Fabales*,

106 and sub-family *Papilionaceae* (Pierozzi et al. 2008). The high nutritional value of soybean

107 makes it an indispensable crop, ranked 6th in terms of total crop yield and the most cultivated

108 oilseed crop which adapts to varied climatic conditions (Kim et al. 2015). The major soybean

109 producers in the world include U.S.A, Brazil, Argentina, China, and India, contributing about

110 90% of global production (Rizzo & Baroni 2018). Soybean possesses several vital nutrients such

111 as carbohydrates, fats, proteins, vitamins, α-tocopherol, and minerals (Table 1). This food crop is

112 widely consumed due to its excellent source of superior quality proteins. Lower levels of blood

113 cholesterol, prevention of cardiovascular disease, breast cancer, osteoporosis in women, and

114 relief of menopausal symptoms are some of the beneficial health effects derived from the

115 consumption of soybean protein (Gutiérrez et al. 2006). Also, continuous consumption might

116 efficiently control aging.

117 Generally, grain legumes are cultivated on marginal lands with less financial resources resulting

118 in low yield. Genetic improvement, fertilizer and pesticide application, coupled with better

119 cultural practices have been employed in an attempt to increase the productivity of these crops

120 (Khan & Mazid 2018). However, particular considerations have not been directed towards the

121 physiological processes which reduce crop productivity. Plant growth regulators (PGRs) could

122 be effective in realizing the yield potentials of these crops due to their numerous effects on plant

123 life including flowering, growth, ion transport, and fruiting (Ali & Bano 2008). Again, PGRs

124 regulate the expression of endogenous hormones, improve plant physiology metabolism, and

125 increase crop yield (Zeng et al. 2012). Especially, PGRs can optimize the process of

126 photosynthesis and play a substantial role in maximizing crop yields. PGRs enhance the

127 transportation of photosynthates, augment the source-sink association and thus, improve

128 productivity (Khan & Mazid 2018). Although PGRs have pronounced potentials, their

129 application and accumulation must be carefully designed with regards to the specific species,

130 optimum concentration, climatic conditions, and the stage of growth. Effective application on

131 every facet of plant growth could increase total productivity by 10-15 million tons annually

132 (Khan & Mazid 2018).

133 Plant growth regulators are known to increase yield and bring about the desired growth per unit

134 land and time. PGRs are also essential for germination, flower and root development, seed

135 maturation, storage, and other functional processes in plants (Wu et al. 2017; Yi-Ping et al.

136 2015). In soybean production, PGRs such as auxin, cytokinin, abscisic acid, ethylene, jasmonic

137 acid, salicylic acid, gibberellins, and brassinosteroids among others has been reported to promote

138 growth and productivity (Basuchaudhuri 2016; Dhakne et al. 2015; Giri et al. 2018; Kim et al.

139 2018; Mohamed & Latif 2017; Roy Choudhury, Johns & Pandey 2019; Sudadi & Suryono

140 2015). PGRs sustainably promote root and shoot growth (Kim et al. 2018; Qi et al. 2013;

141 Steffens, Wang & Sauter 2006), enhance water use efficiency (Giri et al. 2018), promote

142 flowering and pod setting (Nagel et al. 2001), increase chlorophyll content (Sun et al. 2016),

143 improve photosynthetic rate (Qi et al. 2013; Travaglia, Reinoso & Bottini 2009), enhance the

144 translocation of photoassimilates (Liu et al. 2019; Sun et al. 2016), increase biomass

145 accumulation (Liu et al. 2019; Mohamed & Latif 2017), and induce tolerance to several abiotic

146   stresses (George, Hall & De Klerk 2008; Hamayun et al. 2010), resulting in enhanced growth

147   and yield.

148   No comprehensive review is available on the effects of growth regulators on the growth and

149   development of the soybean plant. Hence, we decipher current knowledge and possible

150   applications of plant growth regulators in improving growth and yield. Notably, the regulation

151   effects of various PGRs on the physiological, morphological, and biochemical properties as well

152   as yield and quality traits of soybean are discussed in detail. Also, the mitigation effect of PGRs

153   on various abiotic stress conditions to promote the growth and productivity of soybean are

154   conferred. Based on the reviewed studies, we provide possible insights into the current

155   applications of different PGRs that may affect the morphology, physiology, and yield quality of

156   soybean. This article should be of particular interest to readers in the areas of plant physiology

157   and breeding.

158   **1.1 Survey Methodology**

159   An in-depth literature search of relevant academic articles in databases such as PubMed, Web of

160   Science, Science Direct, and Google Scholar as well as the University's databases for books,

161   journals, and reports was used for the compilation of this article. The search results were

162   achieved through the use of phrases like "growth regulators promote soybean growth", "PGRs

163   affect soybean productivity", PGRs influence soybean morphology", "PGRs mitigate abiotic

164   stress in soybean", etc. together with the use of "NOT", "+", "AND", "vs" for a particular search

165   outcome. Generally, our search focused mainly on the effects of plant growth regulators in

166   regulating the growth and development of the soybean plant and subsequently, increasing

167   productivity. Since there has not been such a comprehensive compilation of studies on this topic,

168   relevant related literature including those dating as far back as the late 1970s and 1980s were

169   reviewed but we mainly focused on works from the past 10 years. Closed access articles and

170   pieces of literature unavailable online that had relevant pieces of information were obtained

171   through University's document delivery and inter-library loan services. Finally, the most relevant

172   articles were used.

173   **2.0 Major Growth Regulators**

174   Plant growth regulators are carbon-based compounds either natural or artificial apart from

175   nutrients that perform fundamental roles in the life cycle of plants and alter or restore growth

176   patterns of plants (Davies 2013). Similar chemicals that affect plant growth are also produced by

177   fungi and bacteria and can be used to control plant growth and development (Khan & Mazid

178   2018). When these regulators are applied in lower quantities, they stimulate the natural systems

179   that regulate growth to bring about rapid changes in the plant by either promoting or inhibiting

180   plant growth from germination to senescence, thus, classified as growth promoters and growth

181   retardants. They are commonly classified as phytohormones including; gibberellins, auxins,

182   ethylene, cytokinins, abscisic acid, and synthetic substances that act like or against them. In

183   recent times, other PGRs such as brassinosteroids, strigolactones, salicylic acid, polyamines, and

184   jasmonic acid among others have also been identified to induce physiological responses in plants

185   (Verma, Ravindran & Kumar 2016). In the majority of cases, PGRs affect the balance of plant

186   hormones in treated plants. PGRs usually work together with other growth regulators and their

187   effects overlap with each other. Table 2 summarizes the effects of different growth regulators on

188   the growth and development of soybean as outlined by different authors.

189   2.1 Auxins

190   Auxins are organic phytohormones with morphogen-like physiognomies implicated to

191   coordinate several developmental processes in plants (Strydhorst et al. 2017). Synthetic auxins

192   including 2, 4- dichloro-phenoxyaectic acid (2, 4-D), 2, 4, 5-trichloro-phenoxyacetic acid,

193   Naphthalene acetic acid (NAA), 2-methyl-4-chloro-phenoxyaectic acid (MCPA), and Indole

194   butyric acid (IBA) mimic the physiological responses of Indole acetic acid (IAA, the universal

195   natural auxin) but are not as active as IAA (Rademacher 2015). Auxins enhance physiological

196   processes that directly control plant growth. For instance, low concentrations of auxins promote

197   phototropism, lateral root initiation, gravitropism, vascular development, influence apical

198   dominance (Davies 2010; Rademacher 2015), longitudinal shoot growth (George, Hall & De

199   Klerk 2008), root formation in cuttings (Small & Degenhardt 2018), and regulate root growth by

200   maintaining root stem cell niche (Liu et al. 2017). Exogenous IAA supplementation increased

201   plant height, leaf number per plant, fruit size, and increased seed yield of groundnut, cotton,

202   cowpea, and rice (Kapgate et al. 1989; Kaur & Singh 1987; Khalil & Mandurah 1989; Lee

203   1990). However, high concentrations can negatively affect plants causing oxidative stress,

204   cellular deaths (Flasiński & Hąc-Wydro 2014), and suppress axillary bud development (Shimizu-

205   Sato, Tanaka & Mori 2009). Thus, described as both stimulators and inhibitors of growth

206   depending on the concentration (Harms & Oplinger 1988).

207   2.2 Gibberellins (GA)

208   Gibberellins are a major group of tetracyclic diterpenoid compounds with diverse properties

209   known to influence various plant developmental processes. Gibberellic acid (GA_3) is the most

210   produced and frequently used gibberellin associated with plant growth and development (Gupta

211   & Chakrabarty 2013). GA_3 promotes photosynthesis, seed germination, flowering, stem

212   elongation, leaf growth, and cell division in plant shoot caused by the direct regulation of protein

213   and RNA (ribonucleic acid) synthesis (Hyun et al. 2016). Also, gibberellins boost longitudinal

214   growth caused by the development of meristematic tissues (Rademacher 2015).

215   Exogenously applied GA_3 elevates the activities of some major enzymes such as ribulose-1, 5

216   bisphosphate carboxylase (Rubisco; Yuan & Xu (2001), carbonic anhydrase, and nitrate

217   reductase (Aftab et al. 2010). Recent reports revealed that GA controls some life processes in

218   plants with regards to stress (Hamayun et al. 2017; Wang et al. 2017) and break dormancy in

219   seeds (Gupta & Chakrabarty 2013). Additionally, GA_3 can either reduce or inhibit the effects of

220   water stress during germination and seedling emergence (Kaur, Gupta & Kaur 1998a) and

221   ameliorate the effects of salt stress, hence, maintaining standard growth and development

222   (Hamayun et al. 2010).

223   2.3 Cytokinins

224   Cytokinins are phytohormones synthesized in meristematic organs and tissues (Rademacher

225   2015). Cytokinins regulate diverse physiological and biochemical processes in multiple plant

226   organs, cell proliferation and differentiation, and plant response to stress conditions. The lack of

227   cytokinin may halt the cell cycle and affect cellular activities (George, Hall & De Klerk 2008)

228   due to its cardinal role in plant cell division by directly regulating protein synthesis during

229   mitosis. Cytokinins promote root growth, shoot development from internodes, chloroplast

230   maturity, and initiate callus formation (Carrow & Duncan 2011; George, Hall & De Klerk 2008)

231   and also stimulate plant responses to diverse biotic and abiotic stresses as well as nutrients by

232   preventing cell degeneration, protein synthesis signaling, and augmenting protective enzymes

233   (Carrow & Duncan 2011). Exogenous cytokinin increased pod setting by inhibiting flower

234   abortion in soybean and lupin and ultimately increased yield (Najafian et al. 2009). Dietrich et al.

235   (1995) reported that the exogenous application of cytokinin to maize plants during pollination

236   increased the number of kernels and the total kernel weight per ear by reducing apical kernel

237   abortion. Benzyladenine (BA) application stimulated cell division and elongation, increased

238   flower production, and decreased flower drop (Krug et al. 2006). Daily application of kinetin

239   (Kn; for 5 d starting from 2 d post-anthesis) increased cell division and grain weight to rice

240   (Yang et al. 2003).

241   2.4 Abscisic acid (ABA)

242   Abscisic acid, a key regulator of abiotic stress resistance in plants (Zhu et al. 2017), also

243   functions to coordinate several cardinal growth and developmental processes (Wani & Kumar

244   2015). In plants, ABA is biosynthesized upon exposure to severe stress conditions to induce

245   stress tolerance (O'Brien & Benková 2013). Thus, referred to as the "stress hormone" (Mehrotra

246   et al. 2014). ABA improves osmotic stress tolerance, protein and lipid synthesis, regulates

247   protein synthesis genes, protects plants against pathogens, controls water and ion uptake,

248   morphogenesis, and embryogenesis, breaks seed dormancy, and decreases leaf abscission

249   (Flasiński & Hąc-Wydro 2014; Strydhorst et al. 2017). Exogenous ABA promotes primary root

250   elongation and leaf senescence in plants. For instance, Spollen et al. (2000) reported that the

251   application of ABA caused the primary root elongation of maize at low water potential. In

252   Arabidopsis, ABA promoted leaf senescence and primary root elongation of seedlings (Zhao et

253   al. 2018). Furthermore, exogenous ABA application in rice induced leaf yellowing, a major

254   indicator of leaf senescence (Fang et al. 2008).

255   2.5 Ethylene (ET)

256   Ethylene (C_2H_4) is a multifunctional hormone synthesized by practically all tissues connected

257   with plant growth in the presence of oxygen (Lin, Hsu & Wang 2010). Its effects on growth and

258   development depend on the ABA, cytokinin, and auxin concentration, light, carbon dioxide, and

259   the plant (George, Hall & De Klerk 2008). Based on the plant species, concentration, and time of

260   application, ET may promote, inhibit, or induce growth and senescence (Pierik et al. 2006). For

261   example, low concentrations of ethephon (an ET releasing compound) increased the leaf area of

262   mustard but no observed increase was recorded at high concentrations (Khan et al. 2008). ET

263   promotes the overall growth of plants by regulating secondary metabolites, cell division, cell

264   size, fruit ripening, flowering, stolon formation, and root initiation (George, Hall & De Klerk

265   2008; Schaller 2012). ET in synergy with other growth regulators promotes plant growth and

266   alleviates dormancy caused by environmental conditions (Kępczyński & Van Staden 2012). For

267   instance, high concentrations of cytokinin together with ET promoted root growth (O'Brien &

268   Benková 2013).

269   Research has established that ET promotes growth by increasing tolerance to diverse stress

270   conditions. For instance, the application of ET improved tolerance under waterlogging

271   conditions in rice by inducing the emergence of adventitious roots, aerenchyma formation in

272   roots, and shoot elongation (Ma, Chen & Zhang 2010). ET regulates abscisic acid and gibberellin

273   homeostasis to stimulate growth (Ahammed et al. 2020) and also facilitates plant adaptation to

274   waterlogging stress. ET improved photosynthesis in mustard and wheat plants subjected to

275   salinity stress (Nazar et al. 2014). According to Wang et al. (2020a), ET increased seed

276   germination in alfalfa under salt stress and ameliorated the effects of salt stress on seedlings.

277   ET's role in cell senescence and plant maturation best describes it as an 'aging' hormone

278   (Schaller 2012).

279   2.6 Brassinolide (BL)

280   Brassinolide is a plant growth-promoting steroid and the most significant naturally occurring

281   brassinosteroid due to its effective biological functions and widespread distribution (Li et al.

282   2020). In tomato, exogenous BL significantly improved vegetative growth by increasing

283   root/shoot length and biomass, shoot architecture, and the total chlorophyll (a & b), carotenoids,

284   carbohydrate as well as mineral contents (Nafie & El-Khallal 2000). In potatoes, the application

285   of 24-epibrassinolide (EBL) prolonged dormancy, increased ET production and improved ABA

286   content in buds (Korableva et al. 2002). Also, exogenous BL improved nitrate reductase activity,

287   absorption of nitrate fertilizer, plant height, biomass accumulation, and resistance to adverse

288   environmental conditions in diverse plant species including chickpea, soybean, wheat, lentil,

289   maize, and rice (Ali, Hayat & Ahmad 2007; Anjum et al. 2011; Hayat & Ahmad 2003).

290   2.7 Salicylic acid (SA)

291   Salicylic acid (2-hydroxybenzoic acid) is a phenolic compound synthesized naturally in plants

292   (cytoplasm and chloroplast), most of which are methylated and/or glucosylated (Janda &

293   Ruelland 2015). SA is known for its cardinal functions in regulating various biochemical and

294   physiological processes in plants including photosynthesis, nutrient transport, absorption of ion,

295   stomatal closure, gaseous exchange, protein synthesis, flowering, seed germination, senescence

296   (Davies 2010), and response to biotic and environmental stress (Simaei, Khavari-Nejad &

297   Bernard 2012). For example, the application of SA increased the number of branches, plant

298   height, and overall yield in cotton (Al-Rawi, Al-Ani & Al-Saad 2014). In thyme (*Thymus*

299   *vulgaris* L), the rate of photosynthesis, dry weight, and tolerance to salt stress increased with a

300   similar observation in rosemary (*Rosmarinus officinalis* L; Najafian, Khoshkhui & Tavallali

301   2009). Under various abiotic stress conditions, the exogenous application of SA at lower

302   concentrations (0.05-0.5 mM) significantly increased seed germination and seedling

303   establishment in Arabidopsis and to an extent alleviated the effects of heat and oxidative stress

304   on seed germination (Alonso-Ramírez et al. 2009).

305   SA facilitates the plant's defense response against microbial pathogens by promoting the

306   production of pathogenesis-related (PR) proteins and upregulating its level in response to

307   pathogen attack, hence, associated with plant immunity (Wildermuth et al. 2001). For instance,

308   the exogenous application of SA actuated the production of PR proteins and induced tolerance to

309   the tobacco mosaic virus (TMV) in tobacco plants. This became evident as SA accumulated in

310   the TMV-infected tobacco plants with a similar observation in *Pseudomonas syringae* pv. *tomato*

311   (*Pst*) infected cucumber plants (Raskin 1992). All the above effects were concentration-

312   dependent, in that different application levels stimulated varied results.

313   2.8 Jasmonic acid (JA)

314   Jasmonic acid (3-oxo-2-2′-*cis*-pentenyl-cyclopentane-1-acetic acid), is a derivative of beta-

315   linolenic acid, an essential component of chloroplast membranes belonging to the oxylipins

316   (Mosblech, Feussner & Heilmann 2009). JA is associated with key biological and physiological

317   processes such as growth and development by mediating the transport of photosynthates (Kaplan

318   2012), uptake of nutrients (nitrogen and phosphorus), inducing stomatal opening, and stress

319   response (Wasternack & Hause 2013). JA doubles as a promoter and inhibitor of growth. For

320   instance, exogenous JA suppressed leaf expansion and adventitious root formation in

321   Arabidopsis (Gutierrez et al. 2012), decreased coleoptile growth and plant height in rice, and

322   inhibited ear shoot growth in maize (Riemann et al. 2013; Yan et al. 2012). However, JA was

323   found to positively regulate lateral root formation in Arabidopsis (Cai et al. 2014) and fiber

324   elongation in cotton (Hao et al. 2012). In Safflower, the foliar spray of JA increased the

325   maximum quantum yield of photosystem II (Fv/Fm), relative water content, chlorophyll content,

326   biomass accumulation, and grain yield (Ghassemi-Golezani & Hosseinzadeh-Mahootchi 2015).

327   Furthermore, the exogenous application of JA induced chlorophyllase activity, leaf senescence,

328   and microtubule degradation of soybean plants (Hassanein et al. 2009).

329   The signaling pathway of JA serves as an effective mediator of environmental stress response,

330   mostly oxidative damage and pathogenic infections, and thus, induces the expression of several

331   target genes suited for this function (Gupta et al. 2017). For instance, Faghih, Ghobadi & Zarei

332   (2017) revealed that the exogenous application of JA to strawberry plants subjected to salt stress

333   decreased lipid peroxidation by improving the antioxidant enzyme activity. Also, JA increased

334   the metabolism of glutathione and ascorbate in the leaf tissues of crested wheatgrass subjected to

335   water stress, thereby increasing tolerance to water stress (Shan & Liang 2010). In Arabidopsis,

336   priming with JA increased tolerance to drought by inducing the expression of reactive genes

337   associated with drought stress (Liu & Avramova 2016). JA stimulates the activities of other plant

338   hormones like ABA, ET, and polyamines (Onkokesung et al. 2012). For instance, JA application

339   delayed ABA-mediated inhibition of seed germination in Arabidopsis (Ellis & Turner 2002) and

340   elevated the content of spermidine in barley (Bandurska, Stroiński & Kubiś 2003).

341   2.9 Amine compound

342   Amine compounds are generally categorized into primary, secondary, and tertiary amines

343   depending on the number of amine groups (one, two, and three respectively). In plant growth and

344   development, the majority of research has focused on polyamines and substituted tertiary amines.

345   Polyamines (PAs) are low molecular weight aliphatic nitrogen compounds comprising of two or

346   more amino groups with strong physiological activity (Vuosku et al. 2018). PAs are classified as

347   novel PGRs usually distributed in virtually all living organisms. The main polyamines present in

348   plants include putrescine (Put), spermidine (Spd), thermospermine (Tspm), and spermine (Spm)

349   and are implicated to regulate several biological processes including embryogenesis, fruit and

350   flower development, and senescence (Mustafavi et al. 2018). The distribution of individual

351   polyamines is tissue/organ-specific with some localized in different cells of the same tissue,

352   attributed to their distinctive functions. For instance, Put was revealed as the most prevalent PA

353   in leaves and its levels were three times higher compared to Spd and Spm while the other organs

354   had Spd as the most dominant PA (Takahashi et al. 2018). In carrot, Put and Spm were found to

355   accumulate in the cytoplasm and cell wall respectively (Cai, Zhang & Guo 2006).

356   PAs play pivotal roles in regulating plant defense response to diverse stress signals. For instance,

357   the exogenous application of PA has been reported to increase stress tolerance in plants leading

358   to improved yield (Liu et al. 2007). According to Liu et al. (2007), the genetic modification of

359   plants with polyamine biosynthetic genes enhanced abiotic stress tolerance in the resulting

360   transgenic plants. Put applied exogenously to chickpea, alfalfa, and welsh onion enhanced

361   tolerance to cold, drought, and flooding stress respectively (Nayyar 2005; Yiu et al. 2009; Zeid

362   & Shedeed 2006). The exogenous application of spermine and spermidine improved growth and

363   yield in Arabidopsis and tomato by enhancing tolerance to drought and heat stress respectively

364   (Murkowski 2001; Yamaguchi et al. 2007). PAs were identified to stimulate embryogenesis in

365   Asian ginseng (*Panax ginseng*; Kevers et al. 2000) and promote shoot regeneration in Korean

366   and Chinese radish (Curtis, Nam & Sakamoto 2004; Pua et al. 1996) and chili pepper (*Capsicum*

367   *frutescens*; Kumar et al. 2007).

368   Substituted tertiary amines (STAs) also increase crop productivity by increasing root growth,

369   photosynthetic efficiency, and overall plant vigor (Qi et al. 2013). The most commonly used

370   STAs in crop production include but not limited to 2-(3, 4-dichlorophenoxy) trimethylamine

371   (DCPTA), diethyl-2-(4-methylbenzoxy) ethylamine (MBTA), diethyl aminoethyl hexanoate

372   (DTA-6), and 2-(N-methylbenzylaminoethyl)-3-methylbutanoate (BMVE). Studies have shown

373   a positive yield effect of DCPTA application in tomatoes (Keithly, Yokoyama & Gausman 1990)

374   and a promotive effect on seedling growth and development in radish (Keithly, Yokoyama &

375   Gausman 1992). In another study, seed treatment with 30 μM DCPTA resulted in a significantly

376   enhanced root and hypocotyl elongation along with seedling dry weight of radish (Keithly,

377   Yokoyama & Gausman 1992). Van Pelt & Popham (2007) revealed that the foliar application of

378   DCPTA and MBTA during the two true leaf stage of pepper seedlings did not only increase yield

379   but also significantly improved fruit pigment content. Wang et al. (2016) recently showed that

380   DCPTA application increased plant growth in corn but the resulting stem elongation increased

381   lodging and subsequently decreased yield. However, the combined effect of DCPTA and CCC

382   sprayed at the seedling stage ameliorated the problem of lodging in corn by reducing stem

383   elongation leading to increased yield (Wang et al. 2016). This is because CCC acts

384   antagonistically to gibberellic acid to inhibit stem elongation. Seed treatment with BMVE

385   reportedly increased plant growth and yield in multiple crop species (Yokoyama et al. 2015).

386   According to Qi et al. (2013), the foliar treatment of DTA-6 on the canopy of corn and soybean

387   at the third trifoliate (V3) stage increased plant height, root length, leaf area, dry matter

388   accumulation, root to shoot ratio, along with improved Rubisco and phosphoenolpyruvate

389   carboxylase (PEPCase) activity, chlorophyll content, and the photosynthetic rate which were in

390   line with that observed in radish, spinach, and tomato (Keithly, Yokoyama & Gausman 1992).

391   Furthermore, the application of DTA-6 increased the CO_2 assimilation rate in corn and soybean

392   seedlings as the plants exhibited higher Fv/Fm values than the control and ultimately improved

393   the photosynthetic apparatus.

394   **3.0 Regulation Effects of Different PGRs on Soybean**

395   Application of PGRs control plant development by regulating the endogenous hormone

396   biosynthesis and catabolic system to facilitate the desired growth (Zeng et al. 2012). PGRs have

397   numerous advantages over traditional methods of crop production due to their effectiveness at

398 low concentrations, wide range of applications, low toxicity, ability to regulate plant morphology

399 and physiology, and their influence on many crop species (Saini et al. 2013a). They affect plant

400 growth from embryo development to completion of life cycle and death (Li et al. 2010). The

401 physiological effect of PGRs depends on the time and method of application, the concentration,

402 frequency of application, weather conditions, and state of plant (Dadnia 2011). Several studies

403 suggest the positive effects of growth regulators on the morphology, physiology, yield, and yield

404 quality of crops, especially soybean. The various actions of PGRs in regulating the different

405 aspects of soybean growth and development are summarized in Figure 1.

406 3.1 Effects on soybean morphology

407 Plant morphology generally consists of the root and the shoot systems. The root system

408 encompasses various types of roots, dynamic in morphology and functions. The vital features

409 that describe root morphology include but not limited to the root length and diameter, root

410 surface area (RSA), and root volume (Wijewardana, Reddy & Bellaloui 2019). Other features

411 like the lateral roots, forks, crossings, and tips regulate the root architecture which is also

412 controlled by the distribution and spatial arrangement of the roots in the soil by positioning its

413 foraging activity to regulate water and nutrient absorption. The shoot system also encompasses

414 plant parts above the soil, usually the leaves, the stem, and the branches generally termed as the

415 shoot. This generally determines the plant's height. These two major systems are essential to

416 plants and are highly influenced by PGRs detailed below.

417 3.1.1 Root

418 Botanically, the root of the plant is an underground organ and functions primarily in absorbing

419 soil minerals and moisture and as well offers firm anchorage. Roots, as the central boundary

420 between plants and the surrounding environment, exert key functions in the growth and

421 development of plants (Marschner 2011). Root growth and development directly affect the

422 growth of the soybean plant. With PGRs affecting growth, understanding their influence on the

423 roots is very important.

424 In soybean growth, most root traits arise from the features of the soybean plant rather than the

425 soil unlike in most crops where the root length and weight are dependent on the oxygen content

426 of the soil which is ascertained by the soil porosity (Yang, Wu & Zhang 2001). Soybean roots

427 under various soil parameters such as moisture, temperature, voids can cause variations in root

428 morphology in addition to other environmental factors (Jian, Xiaobing & Guanghua 2002).

429 Conditions such as waterlogging stress and drought highly influence root growth. Waterlogging

430 stress inhibits root growth by decreasing the size of the root whiles drought influences the root

431 architecture through longer lateral root and root hairs development for better water absorption

432 (Kim et al. 2018). Waterlogging fills soil pores which limits gaseous exchange, thus triggering

433 adventitious root formation (Steffens, Wang & Sauter 2006). PGRs are positive promoters of

434 growth, with ET regulating adventitious root formation. The availability of ET and GA_3 triggered

435 a substantial increase in the development and penetration of adventitious roots of several plants

436 (Steffens, Wang & Sauter 2006).

437 In soybean, endogenous GA increased with the application of ET coupled with increased plant

438 height and adventitious root formation, proposing the ability of ET to improve GA accumulation

439 and hence, improve root growth (Kim et al. 2018). The application of 2-chloroethylphosphonic

440 acid (ethephon, ETP) increased the RSA of the soybean plant, providing a higher surface area for

441 water absorption (Kim et al. 2018). ET and GA control the formation, number, and length of

442 adventitious roots synergistically, hence, exogenous ET application boosts GA accumulation in

443 soybean plants which enhance the RSA and improves root growth. Exogenous application of

444   IBA to soybean hypocotyl induced root development by significantly increasing the number of

445   lateral roots (Chao et al. 2001).

446   3.1.2 Shoot

447   The shoot of plants encompasses its stem and leaves. The leaves function to effectively capture

448   photosynthetically active radiation (PAR). Leaf development is thereby well-thought-out as the

449   principal phenomena of growth and shoot morphogenesis during canopy developmental stages in

450   crops. The application of PGRs is often used as a measure to ensure the reduction of lodging

451   incidence by mimicking or changing the production of hormones essential in improving stem

452   structure and increasing yields (Berry & Spink 2012).

453   In soybean, the application of ETP showed greater shoot growth resulting in increased plant

454   height (Kim et al. 2018). The increase may be related to the elongation of internodes and

455   heightened cell division and expansion. Growth regulator treatments increased the leaf area per

456   plant and leaf area index (Manu, Halagalimath & Chandranath 2020). For instance, cycocel

457   treatments enhanced a prolonged assimilation surface area which delayed leaf senescence, hence,

458   retaining more leaves per plant. Also, cycocel reduced chlorophyll degradation, protease activity,

459   and stimulated the synthesis of soluble protein and enzyme (Khalilzadeh, Seyed Sharifi &

460   Jalilian 2018).

461   Cytokinin is known to induce shoot regeneration and elongation. Its application was observed to

462   control shoot branching and stimulate the growth of axillary bud (Shimizu-Sato, Tanaka & Mori

463   2009). Exogenous application of cytokinin alleviated lateral branch inhibition in soybean plants

464   subjected to high-aluminum toxicity, thus, promoting shoot growth (Pan, Hopkins & Jackson

465   1988). Although cytokinin has been observed to increase shoot development in several pants,

466   very little information is available on soybean shoot development, hence, presenting a gap for

467   future research. Soybean cv. BS-3 sprayed with 100 ppm of IAA at three different times

468   increased plant height, number of flowers, pod number, percent of fruit set, seed number per

469   plant, seed yield per plant, and total seed yield (t/ha) (Sarkar, Haque & Abdul Karim 2002).

470   Application of 100 ppm NAA at the flowering stage has been reported to increase the number of

471   branches per plant, plant height, leaf number per plant, average pod weight, leaf area, dry matter,

472   and seed yield (Deotale et al. 1998).

473   3.1.3 Root nodules

474   Root nodules are the nitrogen-fixing cell protrusions that contain Gram-negative bacteria found

475   on the roots of leguminous plants. These protuberances are formed through a process known as

476   nodulation. Nodulation provides atmospheric nitrogen (N_2) needed for the synthesis of nitrogen-

477   containing compounds like nucleic acids and proteins necessary for enhancing plant growth

478   physiognomies, crop yield, and conserve soil fertility (Mangena 2018). According to Ohyama et

479   al. (2011), one element positively influencing soybean productivity is biological nitrogen

480   fixation. However, it is established through research that the root nodules of legumes including

481   soybean fix atmospheric nitrogen into the soil. Several studies have revealed that the exogenous

482   application of PGRs promotes nodule formation (Mishra et al. 1999). By import, plant growth

483   regulators could improve soybean yield as it promotes nodulation (Sudadi & Suryono 2015).

484   Nodule formation in soybean is extremely sensitive to exogenous plant growth regulators such

485   that they intricately regulate nodule development and affect nitrogen fixation. For instance,

486   the addition of L-tryptophan and indole acetic acid to sterile sand media of neutral pH increased

487   the number of nodules (Sudadi 2012). Likewise, the addition of epi-brassinolide to growth media

488   improved nodulation in soybean by increasing the number of nodules per plant. Sudadi &

489   Suryono (2015) reported that L-tryptophan (0.001 mg L^{-1}, 0.1 mg L^{-1}, 1.0 mg L^{-1}) increased the

490   number of root nodules per plant. Similarly, Basuchaudhuri (2016) reported that applying

491   tryptophan and IAA induced root nodulation in soybean. In another study, the exogenous

492   application of 6-Benzylaminopurine (BAP), indole acetic acid, salicylic acid, gibberellic acid,

493   and jasmonic acid increased nodule number per plant compared to untreated plants, though high

494   concentrations of GA_3 (1 μM) and JA (100 μM) significantly decreased nodule number by about

495   70% and 95% respectively. The results revealed that the effect of these growth regulators is

496   concentration-dependent, however, 10nM IAA, 50nM BAP, 10 μM JA, 10 nM, and 100 nM GA_3

497   and 100 μM to 1 mM SA had the best effect and is considered ideal for high nodule numbers in

498   soybean (Roy Choudhury, Johns & Pandey 2019). According to Mens et al. (2018), the

499   exogenous application of cytokinins (BAP, N^6-(Δ^2-isopentenyl)-adenine and *trans*-zeatin) at low

500   concentrations promoted nodule development while high concentrations decreased nodulation in

501   soybean. Seed priming with low cytokinin concentrations (10^{-9} mol/L) promoted nodulation by

502   increasing the total nodule area, thereby improving biological nitrogen fixation under controlled

503   environments (Kempster et al. 2021). By this, it can be suggested that plant growth regulators

504   intricately regulate nodulation and thus, effective nodulation requires strict regulation of the

505   concentration of growth regulators applied.

506   3.2 Effects on soybean physiology

507   Generally, plant physiology encompasses all processes and mechanisms that make a plant

508   functional such as photosynthesis, water utilization, and environmental physiology among others

509   (Hopkins & Huner 2008). These mechanisms control the growth and development of both shoots

510   and roots, resistance to environmental perturbations, and the interaction of factors associated

511   with growth like nutrition, hormones, temperature, carbon, and energy metabolism. In soybean,

512 all the above mechanisms have been researched with this review focusing on how PGRs boost

513 the utilization of hormones, fertilizer, water, enzymes, and photosynthesis

514 3.2.1 Hormone

515 Plants produce chemicals that regulate processes of growth and development like reproduction,

516 continuous survival, and senescence (Mustafa et al. 2016). These endogenous chemical

517 substances known as phytohormones (plant hormones) are a product of plant secondary

518 metabolism, acting as chemical messengers that coordinate a host of signal pathways and

519 regulate varied cellular activities that facilitate plants' response to abiotic stress (Kazan 2015).

520 They also regulate plants' adaptation to environmental stimuli (Fahad et al. 2015) and their

521 application before/during stress exposure may modulate the endogenous hormone levels to

522 activate plants' response to stress (Kaur, Gupta & Kaur 1998b). Fluctuations in levels of the

523 major plant hormones (auxin, abscisic acid, cytokinin, ethylene, and gibberellins) influence all

524 aspects of plant growth (Zhao et al. 2012). These hormones intricately regulate plant growth by

525 either promoting or inhibiting growth from germination to reproductive growth and flowering,

526 hence classified as growth promoters (gibberellins, cytokinin, and auxin) and growth retardants

527 (abscisic acid and ethylene; Nadeem et al. 2019). Under normal growth and environmental

528 conditions, these hormones are naturally synthesized in certain plant parts but their production

529 minimizes when conditions are unfavorable to promote optimal growth and productivity (Zahir,

530 Asghar & Arshad 2001). Synthetic compounds that mimic the activities of plant hormones

531 otherwise recognized as PGRs are exogenously applied to alter the endogenous hormone levels

532 in plants and to augment growth and yield (Mustafa et al. 2016).

533 Plant growth regulators increase endogenous hormones in plants. In soybean, exogenously

534 applied methyl jasmonate (MeJA) increased the abscisic acid content in plants subjected to salt

535   stress, thus, accelerating tolerance to salt stress (Yoon et al. 2009). A report by Hamayun et al.

536   (2015) revealed that the exogenous application of kinetin (Kn) significantly increased the

537   endogenous bioactive gibberellins (GA_1 and GA_4), jasmonic acid, and free salicylic acid contents

538   in soybean plants subjected to salt stress. This was evident as Kn up-regulated the biosynthesis

539   pathways of gibberellins, jasmonic acid, and free salicylic acid unlike the control. Qi et al.

540   (2013) reported that the foliar application of DTA-6 on soybean leaves increased the endogenous

541   hormone (Zeatin Riboside, gibberellins, and indole acetic acid) levels. This increased PEPCase

542   and Rubisco (key photosynthetic enzymes) activity, photosynthetic rate, high biomass

543   accumulation, and consequently increased productivity. In conclusion, exogenous PGRs regulate

544   the endogenous hormone levels to increase plant metabolic processes concerning growth and

545   productivity.

546   3.2.2 Enzyme

547   Enzymes are mostly utilized in both plants and animals as an effective defense mechanism for

548   eliminating reactive oxygen species (ROS). ROS comprises cellular oxidative damage and the

549   build-up of impaired cell components with a concomitant effect on cell function leading to death

550   (Foyer & Noctor 2011). As reviewed by Hasanuzzaman et al. (2020), various enzymes like

551   peroxidase (POD), catalase (CAT), superoxide dismutase (SOD), and glutathione-s-transferase

552   (GST) in addition to non-enzymatic antioxidants such as reduced ascorbate (AsA) and

553   glutathione (GSH) cooperatively reduce oxidative damage under stress conditions (Figure 2).

554   SOD degrades excess ROS by transforming O_2^- to O_2 and H_2O_2 (Bresciani, da Cruz & González-

555   Gallego 2015) whiles CAT catalyzes the conversion of H_2O_2 to H_2O (Furukawa et al. 2017).

556   Both antioxidant enzymes are essential and considered as a preliminary defense mechanism

557   against oxygen toxicity. Ascorbate peroxidase (APX) is a widely distributed antioxidant in plant

558 cells with its isoforms having a higher affinity for H_2O_2 than CAT, rendering APXs as an

559 efficient scavenger of H_2O_2 under stressful conditions (Sharma, Jha & Dubey 2019). GSH is an

560 essential redox molecule found in all living cells and forthrightly associated with maintaining

561 intracellular redox homeostasis and the antioxidative defense system by stimulating ascorbic

562 acid, through the Ascorbate-Glutathione cycle (Wang, Yang & Yi 2012). GSH also plays a direct

563 role as a free radical scavenger due to its ability to react with H_2O_2, $OH^{\bullet}$, and $O_2^{\bullet-}$. In soybean,

564 POD, APX, polyphenol oxidase (PPO), and CAT activities were up-regulated under salinity

565 stress with a significant increase in MDA and hydrogen peroxide. Also, applying PGRs

566 stimulated the expression of these enzymes hence, influencing stress response. PGRs (salicylic

567 acid and nitric oxide) inhibit the production and accumulation of ROS (H_2O_2, $O_2^{\bullet-}$, $OH^{\bullet}$),

568 decrease the lipid peroxidation content and accelerate the production and accumulation of proline

569 under salt stress (Tan et al. 2008). This significantly decreased MDA and increased the total

570 antioxidant activity (which acts as scavengers of ROS and impedes its harmful effects), thereby

571 increasing tolerance to salt stress. In soybean, exogenously applying SA, sodium nitroprusside

572 (SNP), and their combination (SA+SNP) regulated the proline levels and reduced salt-induced

573 oxidative damage marked by a reduction in the MDA content and subsequently, decreased lipid

574 peroxidation and enhanced catalase activity (Simaei et al. 2011). Applying ETP alleviated water

575 stress in soybean plants by up-regulating GST3 and GST8 (Kim et al. 2018). ETP significantly

576 enhanced the expression of GST3 and GST8 at the biochemical and transcriptional level. Hence,

577 an increase in GST3 and GST8 levels heightened GSH activity, reduced reactive oxygen species,

578 alleviated cell damage in photosynthetic apparatus, and enhanced phenotype (Kim et al. 2018).

579 Foliar application of NAA improved nitrate reductase activity in soybean (Senthil, Pathmanaban

580 & Srinivasan 2003). Also, the application of SOD simulation material (SOD_M) and DTA-6

581 increased SOD, CAT, and POD activities in soybean leaves and lowered MDA, resulting in

582 enhanced seed yield and delayed leaf senescence (Zheng et al. 2008). DTA-6 and uniconazole

583 (S3307) increased the POD activity in pods, reduced vital abscission enzyme activity, MDA

584 activities, and lipid peroxidation, thereby enhancing the accumulation and transportation of

585 assimilates as well as antioxidant capacity (Sun et al. 2016). In addition, exogenously applied

586 SNP induced the antioxidant machinery in soybean plants by enhancing various antioxidant

587 enzyme (CAT, SOD, POD, and APX) activities (Jabeen et al. 2021).

588 Brassinosteroids and JA are well known for their antioxidant capacity and their major

589 involvement in regulating the AsA-GSH cycle in plants. These PGRs boost the plant defense

590 system by increasing antioxidant system capacity, enzymatic activity, and upregulating the

591 expression of antioxidant genes (APX, SOD, POD, CAT, and glutathione reductase (GR); Bali et

592 al. 2018). In soybean, seed priming with EBL increased the antioxidant enzyme (CAT, APX,

593 SOD, and GR) activity and the contents of non-enzymatic antioxidants such as AsA, GSH, and

594 glutathione disulfide (GSSG) under salt stress, which improved salt tolerance, biomass

595 accumulation, and subsequently yield (Soliman et al. 2020). Similar results were obtained with

596 exogenous EBL application in salt-stressed soybean plants as reported by (Alam et al. 2019).

597 Furthermore, exogenous 28-homobrassinolide enhanced the AsA-GSH cycle by activating the

598 antioxidant system, marked by improved activities of APX, SOD, CAT, monodehydroascorbate

599 reductase (MDHAR), dehydroascorbate reductase (DHAR), and GR), leading to efficient ROS

600 scavenging in soybean seedlings (Hasan et al. 2020). According to Mir et al. (2018), the

601 exogenous application of JA enhanced the contents of non-enzymatic antioxidants and

602 antioxidant enzyme activity, thereby boosting redox homeostasis and antioxidant capacity in

603 Nickel-stressed soybean plants. Similar results were also reported by Sirhindi et al. (2016). In

604 another study, MeJA treatment increased CAT, SOD, and APX activity and the level of

605 dehydroascorbic acid (DHA) in soybean leaves under cadmium stress thereby ameliorating

606 cadmium toxicity (Keramat, Kalantari & Arvin 2009). Eventually, all these resulted in

607 heightened growth and productivity of the soybean plant.

608 3.2.3 Photosynthesis

609 Photosynthesis is a vital phenomenon in crop production as it provides the energy needed for

610 plant growth and development, thus, regarded as the basis of growth in plants. Murata (1981)

611 reported a relatively high positive correlation between the optimal growth rate and leaf

612 photosynthesis of many crops. However, the growth rate of plants may not directly reflect their

613 photosynthetic rate. Leaf photosynthesis is a vital component of crop biomass production, thus,

614 an essential determining factor of grain yield through canopy photosynthesis. For instance,

615 Connor, Loomis & Cassman (2011) revealed that photosynthesis produces simple carbohydrates

616 from which more complex carbohydrates (proteins and lipids) are obtained to form the dry

617 matter of plants. In soybean, high seed yield results from enhanced canopy photosynthesis after

618 seed germination. It is hypothesized that a decline in canopy photosynthesis significantly

619 reduced soybean productivity, attributed to decreased pod setting (Jiang & Egli 1993).

620 Furthermore, the improved production of assimilates at the fruit development stage in soybean

621 may increase yield. Based on the above results, it can be deduced that enhanced photosynthesis

622 may improve growth, biomass production, and subsequently increase grain yield in soybean.

623 Therefore, improving photosynthesis in soybean is essential as it may increase productivity

624 without altering other genetic factors (Long et al. 2006).

625 Plant growth regulators enhance chlorophyll content, improve the photosynthetic ability, and

626 increase translocation of assimilates from source to sink , thereby increasing biomass production

627   and ultimately yield. Shao et al. (2014) reported a positive correlation between the rate of

628   photosynthesis and chlorophyll content, indicating that chlorophyll content highly influences

629   photosynthesis in plants. However, this relationship is limited in chlorophyll range, in that

630   increased chlorophyll production may not necessarily increase the photosynthetic rate. Generally,

631   cycocel is reported to increase the translocation of photosynthates (Grewal et al. 1993). Foliar

632   spray of cycocel (500 ppm) on soybean leaves at flower initiation (R1), pod initiation (R3), and

633   flower + pod initiation (R1+R3) growth stages increased the chlorophyll content (Devi et al.

634   2011). The marked increment in chlorophyll content improved photosynthesis and greatly

635   enhanced the translocation of photoassimilates to sink organs (seeds) leading to increased

636   biomass accumulation. Similarly, the foliar spray of NAA (40 ppm), SOD_M, DTA-6, and ABA

637   (300 mg/l) on soybean plants increased the rate of photosynthesis and the chlorophyll content of

638   soybean plants (Qi et al. 2013; Travaglia, Reinoso & Bottini 2009; Zhao et al. 2008). The main

639   factors for the enhanced photosynthesis in the DTA-6 treated plants are the increased activities of

640   key photosynthetic enzymes (PEPCase and Rubisco), improved electron transport capacity

641   which elevated the rate of CO_2 assimilation, eventually improving the photosynthetic apparatus.

642   Also, DTA-6 and uniconazole significantly increased leaf photosynthetic ability. The plant

643   growth regulators maintained high photosynthetic activity, increased the photosynthetic rate, and

644   subsequently biomass accumulation due to the enhanced translocation of photosynthates (sucrose

645   and starch) to different organs resulting in improved yield (Liu et al. 2019). Exogenously applied

646   SA maintained the stability of PSII, increased chlorophyll a/b binding proteins (Chla/bBP),

647   Rubisco activase, Rubisco subunits, oxygen-evolving enhancer protein 1 and 2 (OEE1 and

648   OEE2, respectively), ferredoxin NADP reductase (FNR), and photosynthesis-related proteins in

649   soybean. This improved stomatal conductance, photosynthetic rate, and water use efficiency

650   (WUE), hence, increasing photosynthesis. Also, antioxidant enzyme activity increased with SA

651   treatment (Sharma et al. 2018). These findings suggest that plant growth regulators enhance

652   photosynthesis in soybean by increasing the chlorophyll content, distribution of photosynthates,

653   and biomass accumulation which eventually improves growth and yield.

654   As recently reviewed by Müller & Munné-Bosch (2021), hormonal crosstalk positively regulates

655   photosynthesis in plants. For instance, the exogenous application of IAA caused a marked

656   increase in endogenous JA and ABA levels leading to significantly higher chlorophyll contents,

657   thus, elevating the rate of photosynthesis in clover (Zhang et al. 2020). Furthermore, exogenous

658   BAP increased endogenous zeatin levels which enhanced the F_v/F_m, ΦPSII (relative quantum

659   yield of PSII), and electron transport rate in wheat (Yang et al. 2018). In soybean, MeJA

660   treatments resulted in elevated levels of ABA which increased the photosynthetic rate (Yoon et

661   al. 2009). Furthermore, the foliar spray of DTA-6 increased endogenous Zeatin Riboside,

662   gibberellins, and IAA levels which increased PEPCase & Rubisco levels and the rate of

663   photosynthesis in soybean. This enhanced biomass accumulation, thereby improving

664   productivity (Qi et al. 2013). Though there is extensive research to support the positive

665   regulation of hormonal crosstalk on photosynthesis in several plants, that of soybean is limited,

666   thus, presenting a gap for future research.

667   3.2.4 Water utilization

668   Water utilization is very essential in the growth of plants. Every level of development requires a

669   certain amount of water which is mostly dependent on the season, place and time of planting, and

670   the cultivars involved. The sufficient quantity of water available at these times of growth and

671   development is essential for the diverse parameters of growth such as seed weight and size

672   among others.

673 Generally, water use efficiency (WUE) defines the quantity of carbon assimilated as biomass

674 produced per unit of water used by the plant. Hence, WUE is expressed as the relationship

675 between yield/biomass to the soil water evaporation component and the transpiration component

676 which together denotes Evapotranspiration (ET) or the overall water available to the crop,

677 comprising precipitation and the quantity of water available through irrigation i.e. Yield

678 $= ET * WUE$ where $ET = T_{soil} + T_{crop}$ (Kuglitsch et al. 2008). Understanding the crop water use

679 was further detailed down by analyzing the water use at the leaf and canopy level. The leaf level

680 WUE was expressed as the net photosynthetic rate (A_n) divided by the transpiration rate (E)

681 (Hatfield & Dold 2019). In soybean, analysis of WUE at leaf and field scales revealed that a 1%

682 increase in leaf-scale WUE showed ~10% increment in field-scale explaining the 90% yearly

683 variability in field-scale (Gorthi 2017). WUE can hence be utilized as secondary criteria for

684 selecting seed yield genotypes.

685 PGRs, being popular for their influence on various morphological and physiological parameters

686 of plants, have limited information regarding water utilization in soybeans. According to Kamal

687 et al. (1998), the foliar application of 2-ppm S-abscisic acid on soybean at the reproductive stage

688 increased seed yield, pod number, and seed number under conditions of optimal or moderate

689 water stress whereas severe conditions reduced seed yield. The WUE of soybean was enhanced

690 after the application. GA_3 application during flowering and pod development, significantly

691 increased rainwater use efficiency and productivity (Giri et al. 2018). This then proposes that

692 GA_3 application enhanced the effective use of water by the soybean plant which was reflected in

693 the increment in its yield.

694 3.2.5 Fertilizer utilization and nitrogen fixation

695 Nitrogen is a key nutrient for plant growth. Generally, legumes can fix nitrogen in soils which

696 are further utilized by the plant for growth (Wang et al. 2020b). Di-nitrogen (N_2) fixation by

697 leguminous crops has attracted much interest in recent times due to the nitrogen nutrition it

698 provides in a highly sustainable and economically competitive way hence, participating in

699 environmentally sound agricultural production as well as high-quality crop products (Vollmann

700 et al. 2011).

701 In soybean, an increase in growth and yield have been reported to be dependent on large inputs

702 of nitrogen with the pod initiation (R3) to full seed (R6) growth periods, requiring higher N

703 contents (Oplinger 1991). Despite this high requirement of nitrogen, only 25-60% of this

704 nitrogen is naturally available with the rest compensated for by the application of nitrogen

705 fertilizer to the soil. Although there have been several conflicting reports on the benefits of

706 applying nitrogen fertilizer for soybean yield, it has been firmly agreed that soybean plants act as

707 sinks for soil nitrogen and utilize it effectively (Varvel & Peterson 1992). The effective

708 utilization of this soil nitrogen increased yield during the early pod filling stage (Oplinger 1991).

709 However, increasing soil nitrogen at planting reduces soybean response to N fertilizer (Stone,

710 Whitney & Anderson 1985).

711 Despite all the benefits stated by several researchers about exogenous nitrogen application, it can

712 be observed that the benefits were directly related to the timing of nitrogen application. For

713 instance, the application of N fertilizer during planting reduced nodule formation, increased grain

714 yield at flowering and early pod fill growth stages (Oplinger 1991). Also, the starter N

715 application at the beginning flowering/flower initiation (R1) stage did not influence the

716 protein/oil concentrations or increase yield but increased the dry matter content and plant N

717   content (Wood, Torbert & Weaver 1993). At the beginning seed (R5) stage, N increased grain

718   yield, dry matter accumulation, seed protein concentration but reduced seed oil concentration. In

719   all, with N fertilizer application improving soybean growth during the early season, it can hence

720   be proposed that application at this stage is beneficial to the soybean plant and its nitrogen

721   content, however, for effective utilization of the applied fertilizer, the R5 stage may be the most

722   reliable. The above results, however, may not be independent of other factors. Per speculations,

723   environmental factors may limit soybean growth by restricting N fixation, which may result in a

724   positive response to N fertilizer. Hence, factors such as nitrogen concentration, cultivar, and

725   environmental parameters may be responsible for several conflicting reports in terms of fertilizer

726   utilization in soybean plants.

727   Despite all the above reports, one major limitation is the fact that the above researches were

728   conducted one to three decades ago. Current information on fertilizer utilization is however very

729   limited with none on how PGRs regulate fertilizer utilization. However, from knowing the

730   various impacts and limitations of PGRs and fertilizers, the following hypothesis can be made.

731   With the majority of PGRs involved in improving growth and yield, their application together

732   with N fertilizers might enhance growth and yield in double folds than the individual increases

733   and probably reduce the negative effects such as the low nodule formation at the planting stage.

734   A study by Devi et al. (2011) indicated that applying the required amount of NPK fertilizer at

735   planting before applying various PGRs (50 ppm Salicylic acid, 200 ppm Ethrel, and Cycocel) at

736   three different stages of development (R1, R2, and R1+R2) increased growth, yield and yield

737   components, photosynthetic pigments, and protein and oil contents. Although it was not

738   categorically stated that the result was due to the fertilizer application, there is a possibility of the

739   fertilizer playing a role and revealing the chance of our hypothesis being true. This hypothesis,

740   however, needs to be thoroughly investigated to reach a conclusive finding.

741   3.3 Effects on soybean yield, yield components, and quality

742   In soybeans, the yield production process highlights those processes and features that play vital

743   roles in defining yield. These features, mostly termed as the yield component includes seed

744   biomass, pod number, seed number, and seed size, among others. The quality of the soybean also

745   defines a successful harvest and yield.

746   3.3.1 Yield and yield components

747   Major evidence of the extent of growth in plants is their yield. The yield is hence known as the

748   productivity or output of the plant. Several traits of the plant known as the yield components

749   cumulatively determine the overall yield. In soybean, components such as pod number, seed

750   weight, seed number, and population density among others contribute to the overall yield and an

751   increase in these components may significantly influence the yield. Enhancing these components

752   and subsequently, the overall yield requires the adoption of various agronomic practices such as

753   the application of plant growth regulators.

754   Numerous researches have studied the influence of PGRs on these components and their

755   influence on the overall yield of plants. Applying NAA revealed an increment in the yield of

756   soybean (Basuchaudhuri 2016). Seed yield, pod number per plant, and overall yield of soybean

757   increased after NAA application (between 10-100ppm; Dhakne et al. 2015). A larger pod and

758   seed number per plant were also recorded in soybean treated with 250 ppm of CCC resulting in

759   higher seed yield (Kumar et al. 2002). Soaking seeds with 10 ppm gibberellic acid before

760   sowing, then spraying again at the vegetative and flowering stage recorded a significant increase

761   in yield (2.62 tons per hectare; Domingo 1981). Soybean plants treated with 300 mg/l of BA

762 decreased pod abortion in the lower, middle, and upper third of the canopy resulting in high

763 productivity (Borges, Junior & de Freitas Santos 2014). BAP application to racemes before

764 efflorescence, reduced flower and pod number whereas application around 7 d after

765 efflorescence considerably improved the rate of pod set (Nonokawa et al. 2007). The time of

766 application can affect the productivity of the soybean plant, thus application during the end of

767 flowering is more advantageous for soybean cultivation.

768 A study involving the foliar application of Tri-iodo benzoic acid (TIBA) to the soybean plant

769 revealed an enhanced pod number per node (Noodén & Nooden 1985). Also, Kumar et al. (2002)

770 detected a substantial increase in the pod and seed number per plant when 50 ppm of TIBA was

771 applied and consequently increased the grain yield in soybean. Treatment with 15 to 120 ppm

772 TIBA facilitated fruit development and better conditions for podding and also increased seed

773 yield. However, higher levels were injurious to the plant (Buzzello et al. 2013). Again, seed

774 yield, weight, and harvest index were observed to increase in soybean cv. Harit Soya when

775 treated with 20 ppm GA_3 at bud initiation and 50% flowering stage (Upadhyay & Rajeev 2015).

776 Higher concentrations of GA_3 at 100 ppm efficiently augmented the number of pods and seeds

777 per plant, seed weight per plant, and the overall seed yield of soybean (Sarkar, Haque & Abdul

778 Karim 2002). Soybean cv. JS-9305 saw a significant increase in the seed and pod number per

779 plant, seed weight, and total yield when seeds were primed (Agawane & Parhe 2015). Different

780 concentrations of GA_3 significantly influenced the pod number per plant, seeds per pod, 1000

781 seed weight, and economic yield of soybean (Dhakne et al. 2015).

782 Nagel et al. (2001) revealed that the exogenous application of cytokinin improved the total yield

783 of soybean by increasing the pod and seed number per plant. Total seed production increased

784 with increasing cytokinin concentration, suggesting that the total yield of soybean may depend

785   on cytokinin levels. Foliar application of plant growth regulators at both R1 and R3 stages

786   decreased flower drop and efficiently influenced the transport of assimilates from source to sink.

787   This, however, increased the pod number per plant significantly in many crops (Copur, Demirel

788   & Karakuş 2010). In soybean, applying GA_3 at the R1 and R3 stages significantly increased the

789   pod number per plant.

790   Also, PGRs increased pod length which determines the seed per pod of soybean plants,

791   depending on the time of application. For instance, the application of salicylic acid at the R1

792   stage and GA_3 (foliar) at the R1+R3 stages recorded the highest pod length in soybean compared

793   to other treatments applied at different stages of growth (Khatun et al. 2016). According to

794   Dhankhar & Singh (2009), applying GA_3 increased the pod length of the soybean plants. The

795   seed number per pod increased with the application of salicylic acid and Kn spray at vegetative,

796   R3, and R1+R3 stages which were the same for the foliar application of GA_3 at the R1+R3 stage.

797   The application of salicylic acid and 100 ppm GA_3 had the best effect. Similarly, Devi et al.

798   (2011) recorded an increase in the seed number of soybean with the application of 50 ppm

799   salicylic acid at the R1+R3 stage. Foliar spray with 50 ppm salicylic acid and 200 ppm of ethrel

800   applied at R1, R2, and R1+R3 growth stages in soybean cv. JS 335 increased seed yield,

801   attributed to better vegetative growth (Devi et al. 2011).

802   Further researches have reported the application of PGRs to increases the seed weight of

803   soybean. Zholobak (1986) recorded a 20% increase in 100-seed weight when Kn was applied

804   compared to the control. Similarly, Khatun et al. (2016) recorded the highest 100-seed weight in

805   soybean with the application of salicylic acid and Kn spray at the R1+R3 and R3 stages

806   respectively. Similar results were recorded for the foliar application of Kn at the vegetative stage.

807   Devi et al. (2011) also reported an increase in the 100-seed weight of soybean with the

808   application of Kn (500 ppm) at the R1+R3 stage. Kn application (40ppm) also increased the total

809   pod set per plant, net return, and yield of soybean respectively with high concentrations

810   recording the highest yield (Passos et al. 2011). This increase is attributed to the ability of plant

811   growth regulators to improve photosynthesis and enhance the translocation of photosynthates in

812   reproductive sinks of soybean plants which increased the cumulative effect of yield components

813   and subsequently, increased the overall yield of soybean. However, the time of application of the

814   growth regulators significantly influenced the 100-seed weight of soybean.

815   These results project that flower and pod dropping of soybean can be minimized by using

816   exogenous BA, GA$_3$, Kn, and SA. Also, these PGRs can influence the diverse yield components

817   which intend to affect the overall yield by restricting stress impacts. Under various

818   environmental stresses, the application of PGRs may reduce the effects of these stresses on

819   growth and overall yield. For instance, under salt stress, foliar application of n-triacontanol

820   increased the specific leaf area (SLA) by increasing the leaf osmotic potential which may be due

821   to increased organic solutes (Na$^+$ and Cl$^-$) in the leaves (Dhakne et al. 2015). One detrimental

822   effect of salt stress in plants is to induce a reduction in relative water content of leaves, leading to

823   loss of turgor which makes available little water for cell extension processes (Krishnan &

824   Kumari 2008). However, the foliar application of n-triacontanol alleviated this effect and

825   increased the SLA. Also, exogenous ABA increased soybean yield under water deficit conditions

826   (Zhang et al. 2004).

827   3.3.2 Quality

828   Mostly, the nutritional constituents of plants describe their quality. Research evidence suggests

829   that plant growth regulators significantly increase the nutritional value/quality of soybean seeds.

830   Seed quality parameters like protein content are of special concern to food-grade soybean

831   production. Low protein content in soybean seeds is undesirable for soymilk as well as tofu

832   yield. Soluble protein has essential functions in plant growth and is a key constituent of several

833   plant enzymes reflecting the plant's metabolism in totality. Foliar applications of 100 mg/l

834   salicylic acid, 10 mg/l paclobutrazol (PP$_{333}$), or 5 g/l humic acid to soybean plants had a positive

835   influence on maximizing its nutritional value (El-Aal & Eid 2017). Salicylic acid at 50 ppm

836   increased the quality of soybean and yield components compared to the control (Devi et al.

837   2011). Treating plants with GA$_3$ reduced seed protein whiles GA$_3$ spray increased oil content

838   (Travaglia, Reinoso & Bottini 2009). Higher doses of NAA also resulted in larger seed size and

839   high protein contents but lower oil contents in soybean (Basuchaudhuri 2016). Exogenous

840   cycocel application increased protein and oil contents in soybean seeds (Devi et al. 2011).

841   Although the application of PGRs influenced the nutritional value of the soybean plant, the time

842   of application played an essential role. Application of GA$_3$ and salicylic acid (spray) significantly

843   improved the protein percentage of soybean with the highest protein percentage recorded for

844   GA$_3$ application at R1+R3 stage and salicylic acid (spray) at the vegetative, R1, and R3 stages

845   (Khatun et al. 2016). Although GA$_3$ did not greatly influence the oil content, application during

846   flowering and pod development showed a significant increase. The increase in the oil yield

847   correlated directly with the grain yield of soybean (Giri et al. 2018). Furthermore, spraying

848   salicylic acid on leaves and stems of soybean cv. BARI at the vegetative, R1, R3, and R1+R3

849   stages also increased the protein and moisture content of seeds (Khatun et al. 2016). In a recent

850   study, foliar application of JA (0.5 mM) and SA (1 mM) enhanced the oil quality and yield as

851   well as the fatty acids of soybean seeds by increasing the unsaturation index (UI), linolenic acid,

852   and linoleic acid contents while reducing the oleic acid content. SA had the best effect on oil

853   quality and yield both under salt toxicity and normal conditions (Ghassemi-Golezani &

854 Farhangi-Abriz 2018). Moreover, the floral application of exogenous MeJA (0.1 mM) and SA

855 (0.1 mM) increased the isoflavones content in soybean seeds (Saini et al. 2013b). Similarly,

856 Hamayun et al. (2015) reported a significant increase in the isoflavones content of soybean with

857 the exogenous application of Kn which enhanced their biosynthesis directly by upregulating the

858 expression of key pathway genes. Taken together, PGRs have the potency of enhancing the

859 quality of soybean seeds both under stressed and normal conditions.

860 3.4 Effects on biotic stress

861 Biotic stress results from damages caused by living organisms such as bacteria, viruses, fungi,

862 insects, nematodes, and weeds. These organisms subject crop plants to several kinds of infections

863 and diseases which diminishes plant vigor and in severe conditions, death as a result of direct

864 nutrient deprivation (Gull, Lone & Wani 2019). Plants effectively combat the detrimental effects

865 of biotic stresses through their inducible defense mechanisms, mostly controlled by

866 phytohormones such as SA, JA, ABA, ET, and BR (Koo, Heo & Choi 2020).

867 Exogenous phytohormone supplementation enhances plant defenses against pathogenic diseases.

868 For instance, application of PGRs such as SA, IAA, IBA, NAA, GA_3, BAP, Kn, BTH (a

869 synthetic SA analog), and 2, 4-D inhibit sporulation, mycelium growth, mycotoxin synthesis,

870 germ tube elongation, toxin production, aflatoxin synthesis, pathogenicity, and growth of

871 pathogens including *Aspergillus spp. (umbrosus*, *parasiticus*, and *nidulans*), *Nigrospora spp.*

872 (*oryzae* and *sphaerica)*, *Botrytis spp.* (*cinerea* and *allii), Penicillium expansum, Colletotrichum*

873 *dematium*, *Alternaria alternata*, *Xanthomonas oryzae* pv. *oryzae* (*Xoo*), *Sclerotinia sclerotiorum*

874 and *Magnaporthe oryzae* among others (Abass 2017; Bucio-Villalobos et al. 2005; Qin et al.

875 2003). The growth inhibition reduced disease incidences such as mold disease in cucumber

876 (Al-Masri et al. 2002), early blight in potatoes (Michniewicz & Rozej 1988), botrytis blight in

877 cut rose flowers (Shaul, Elad & Zieslin 1995), and improved resistance to bacterial leaf blight

878 and blast disease in rice (Shimono et al. 2007). Furthermore, exogenously applied JA, SA, ET,

879 and Kn induced resistance to root-knot nematodes in rice by upregulating PR genes (Nahar et al.

880 2011) and inhibited the penetration and growth of root-knot nematodes in tomatoes (Dropkin,

881 Helgeson & Upper 1969). In addition, 2,4-D was used as herbicide to effectively eradicate

882 broad-leaved weeds, triggered by uncontrollable cell division leading to death.

883 In soybean, exogenously applied BTH and 1-aminocyclopropane-1-carboxylic acid (ACC, an ET

884 analog) significantly induced resistance to *Phytophthora sojae* which causes the Phytophthora

885 root and stem rot disease by enhancing the expression of PR genes (Sugano et al. 2013).

886 Similarly, ACC treatment inhibited hyphal growth of *Phytophthora sojae* and suppressed disease

887 incidence in excised hypocotyls and cotyledons, respectively (Park et al. 2002). Dann et al.

888 (1998) reported reduced severity of white mold disease caused by *Sclerotinia sclerotiorum* after

889 BTH application. Furthermore, exogenously applied MeJA decreased root-knot nematode

890 (*Meloidogyne spp.*) infections by significantly reducing nematode population (Hu et al.

891 2017). Similarly, MeJA applications reduced soybean cyst nematode (*Heterodera glycines*)

892 infections by upregulating the expression of (E, E)-a-farnesene synthase gene in soybean roots

893 (Lin et al. 2017). Thus, exogenous JA might be an alternative strategy to induce soybean

894 resistance against nematode infections. However, the actions of these growth regulators were

895 concentration-dependent (Al-Masri et al. 2002).

896 3.5 Effects on abiotic stress

897 Abiotic stresses such as salinity, drought, and severe temperatures negatively affect the

898 morphology and physiology of plants by affecting the gene regulatory mechanism of cellular

899 pathways (Egamberdieva et al. 2017). PGRs are chemical messengers that act in very small

900   quantities to arbitrate abiotic stress response in plants. Exogenous application of these growth

901   regulators offers an alternative approach to control abiotic stress which decreases plant growth

902   and productivity (Wani & Sah 2014). Several abiotic stresses including waterlogging, drought,

903   low temperature, and salt stress negatively influence the growth and development of soybean

904   plants, however, different growth regulators have successfully mitigated these stress factors

905   leading to improved growth and productivity in soybean (Figure 3).

906   3.5.2 Low temperature

907   Low temperature, one of the major limiting factors of plant growth and productivity, is defined

908   as a drop in temperature to a level low enough but not freezing (> 0 °C) to influence cellular

909   function, abnormalities at various levels of cell organization, and inhibit growth. Membrane

910   damage, reduced cellular respiration, and enhanced ROS production is the characteristic effects

911   of low temperature in plants (Xing & Rajashekar 2001). In soybean, all growth and

912   developmental stages (from sprouting to seed filling and maturity) are negatively affected by low

913   temperature, making soybean a cold-sensitive plant (Holmberg 1973).

914   Low temperature reduces the rate of germination in soybean by delaying germination, that is, the

915   lower the temperature, the lesser the rate of germination. Several studies have reported the

916   adverse effects of low temperature on pod set and seed yield in soybean due to major factors

917   such as poor growth, abscission of flowers and pods, and inadequate seed filling (Matsukawa

918   1994). For instance, low-temperature treatment before and during flowering resulted in ruinous

919   pod abscission in soybean (Michailov 1989). Funatsuki et al. (2004) recorded a high reduction in

920   soybean yield resulting from malformed pods and reduced seed filling upon exposure to low

921   temperature before and during flowering. Furthermore, exposing soybean plants to low-

922   temperature stress before flowering decreased the rate of fertilization and pod set marked by a

923   decline in male fertility (Goto 1972), attributed to the abnormal development of pollen grains,

924   decreased pollen dispersal, and reduced number of pollen grains on the stigma (Ohnishi, Miyoshi

925   & Shirai 2010). According to Kurosaki & Yumoto (2003), long-term exposure of soybean to low

926   temperature diminished pod set caused by a decline in the number of fertilized flowers which

927   severely influenced grain yield. Similarly, Ohnishi, Miyoshi & Shirai (2010) revealed that low-

928   temperature stress significantly decreased pod set at the flowering stage (12.5 d and 3-4 d before

929   anthesis) by disrupting the normal development of pollen grains, pollen dispersion, reduced

930   number of pollen grains deposited on stigma and subsequently reducing pollination. However,

931   the response to low temperature at the flowering stage and the pod setting capacity upon

932   exposure to low-temperature stress is cultivar dependent, mainly based on the tolerance level

933   (Kurosaki & Yumoto 2003).

934   To eliminate the detrimental effects of low temperature on the growth and productivity of

935   soybean, and further improve tolerance to low temperature, plant growth regulators have been

936   demonstrated through several studies as an effective agronomic technique. In soybean, tolerance

937   to low temperatures has been achieved through the exogenous application of PGRs, and this

938   promoted growth and seed yield. For instance, low concentrations of 5-aminolevulinic acid

939   (ALA) induced low-temperature tolerance in soybean plants by improving heme-catabolism and

940   antioxidant enzyme (heme-catalase (CAT) and heme- oxygenase-1 (HO-1)) activity. These

941   enzymes inhibited oxidative damage by scavenging ROS, thereby protecting soybean plants from

942   the ravaging influence of low-temperature stress. Pre-treatment with 5 µM of 5-aminolevulinic

943   acid before cold treatment had the best effect (Balestrasse et al. 2010). Based on the results

944   outlined above, it can then be proposed that the exogenous application of PGRs enhance soybean

945   tolerance to low temperature and may be useful in preventing yield losses due to low

946   temperatures.

947   3.5.3 Salt stress

948   Salt stress as an abiotic stress factor embraces all salt-related problems emanating from the

949   abundant supply of NaCl (sodium chloride) either by natural accrual or artificial supply through

950   irrigation (Flowers & Flowers 2005). Salt stress has overwhelming effects on the overall growth

951   and development of plants by affecting numerous vital physiological processes in plants (El

952   Sayed & El Sayed 2011) like protein synthesis, photosynthesis, and energy metabolism (Ahmad

953   et al. 2019). Generally, salt stress interferes with complex hormone interaction, ion toxicity,

954   osmotic effects, and nutritional imbalances in plants (Ahmad et al. 2019).

955   In soybean, salt stress disrupts overall growth and development (Phang, Shao & Lam 2008) by

956   influencing photosynthesis, seed germination, nutritional imbalance, nutrient uptake, and

957   productivity (Zhu 2016). For instance, Shu et al. (2017) indicated that salt stress impedes

958   germination by dwindling the GA/ ABA ratio in soybean. Similarly, Kumar (2017) indicated a

959   decrease in germination and seedling growth in soybean under salt stress. Khan et al. (2016) and

960   Ghassemi-Golezani et al. (2010) reported a significant reduction in all yield-related traits under

961   salt stress and eventually caused a significant decrease in the final yield of soybean. Ruzhen &

962   Yiwu (1994) recorded nearly 40% yield loss in soybean as a result of the high soil salinity. A

963   recent study reported a decline in the amount of grain oil and seed protein of soybean under salt

964   stress. In contrast to the control, the oil and protein contents diminished as the salt concentration

965   escalated (Ghassemi-Golezani et al. 2010). In another study, Egbichi et al. (2013) reported that

966   exposing soybean plants to salt stress-induced oxidative damage of membrane lipids in the root

967   nodules.

968   Several techniques such as conventional breeding and exogenous application of PGRs have been

969   reported to enhance plants' tolerance to salt stress, promote plant growth, and consequently

970   increase productivity (Javid et al. 2011). Though soybean plants are adapted to several

971   mechanisms that induce resistance to salt stress, agronomic techniques to eliminate salt stress in

972   soybean are minimal. Plant growth regulators offer a lasting solution to the many growth

973   challenges faced by soybean plants under salt stress. The exogenous application of fluridone

974   (FLUN) promoted seed germination of soybean under salt stress by inhibiting the biosynthesis of

975   ABA and promoting GA biosynthesis (Shu et al. 2017). Exogenously applied Kn ameliorates the

976   adverse effects of salt stress by declining the levels of ABA (growth inhibitory hormone) and

977   elevating the GAs and SA (growth and defense hormones) levels. These endogenous hormone

978   fluctuations caused by the influence of exogenous Kn, significantly increased the fresh weight,

979   plant height, and dry weight of soybean plants thereby promoting growth through enhanced

980   chlorophyll content and leaf area (Hamayun et al. 2015). In another study, the combined effect of

981   exogenous SA and SNP, a nitric oxide (NO) donor significantly improved shoot biomass (both

982   fresh and dry), and the leaf area of soybean plants under salt stress by increasing the chlorophyll

983   content. This stimulated the photosynthetic ability of the soybean plants and subsequently

984   improved growth. However, 100 mM salicylic acid and/or 100 μM sodium nitroprusside had the

985   best effect (Simaei et al. 2011).

986   Plant growth regulators, whether single or combined can alleviate salt-induced oxidative damage

987   and confer resistance to salt stress (Dong et al. 2017). According to Krishnan & Kumari (2008),

988   foliar spray of n-triacontanol (TRIA, a saturated primary alcohol) reduced the harmful effects of

989   salt stress on soybean plants and promoted growth. This was evident with the observed increase

990   in all growth parameters (fresh weight, dry weight, root and shoot length), physiological

991   parameters (relative water content, SLA, and leaf weight ratio), and biochemical parameters

992   (total soluble sugars, soluble proteins, nucleic acids (DNA and RNA) and chlorophyll content)

993   tested. The accelerated growth seen in soybean plants resulted from enhanced cell division and

994   expansion (Sun et al. 2016), increased nutrient content (K^+ and Ca^{2+}) and its metabolism which

995   enhanced the absorption of Na^+ ions (Song et al. 2016), increased nitrogen availability (Parashar

996   & Verma 1993) and decreased chlorophyllase and protease activity (Dong et al. 2017). Thus,

997   suggesting the ability of n-triacontanol to restore normal metabolism in salt-stressed soybean

998   plants. Although growth was accelerated, there was a decline in proline accumulation and leaf

999   osmotic potential. From the above report, it is speculated that plant growth regulators can

1000   ameliorate the adverse effects of salt stress on soybean plants and accelerate growth, thereby

1001   increasing productivity.

1002   3.5.1 Drought

1003   Drought stress is characterized by low atmospheric and soil humidity as well as high ambient

1004   temperature influenced by an imbalance between water intake from the soil and

1005   evapotranspiration oscillations (Lipiec et al. 2013). Drought stress is detrimental to the growth

1006   and development of plants by influencing their biochemical, morphological, physiological, and

1007   genetic resources which diminishes productivity (Khan & Mazid 2018). Thus, drought hinders

1008   the proper functioning of plants by interrupting the water use potential and turgidity. Moreover,

1009   drought influences oxidative damage which may degrade proteins, lipids, nucleic acids, and

1010   cause lipid peroxidation in plants (Lipiec et al. 2013).

1011   Soybean is a drought-sensitive crop and its exposure to drought stress particularly during seed

1012   filling (Desclaux, Huynh & Roumet 2000), flowering, and pod-filling stages (Kobraee, Shamsi &

1013   Rasekhi 2011) reduces photosynthesis, thus, decreasing yield (Liu, Jensen & Andersen 2004).

1014   During drought stress, the rate of abortion at the early pod-filling stage increases in soybean and

1015   thus affect productivity (Lie, Anderson & Jensen 2003). In soybean, water stress including

1016   drought stress approximately caused a 40-60% yield loss (Ahmed et al. 2013). Shou et al. (1991)

1017   recorded a 46% and 20% decrease in soybean yield at the flowering and seedling stages

1018   respectively due to decreased photosynthesis under water stress.

1019   In an attempt to increase soybean growth and productivity under drought conditions, many

1020   drought-tolerant soybean varieties have been developed through conventional and molecular

1021   breeding technologies. Another optional approach by researchers to effectively promote plant

1022   growth and increase drought tolerance is the application of growth regulators. Exogenous

1023   application of PGRs such as abscisic acid, brassinolide, and uniconazole under drought

1024   conditions increased soybean tolerance to drought stress and improved productivity. For

1025   instance, uniconazole application under drought stress improved soybean tolerance to drought

1026   which increased biomass accumulation and seed yield (Zhang et al. 2007). The higher yields

1027   recorded in uniconazole-treated soybean plants may be as a result of the enhanced transport of

1028 ^{14}C assimilates from leaves to pods. Zhang et al. (2008) indicated that treatment with BL before

1029   drought stress minimized water-deficit yield loss in soybean. In another study, foliar application

1030   of MeJA eased drought stress in soybean plants thereby improving drought tolerance and yield in

1031   comparison to unstressed plants (Mohamed & Latif 2017). The drought tolerance exhibited by

1032   soybean plants treated with MeJA (foliar spray) is ascribed to the elevated levels of soluble

1033   sugars and secondary metabolites including flavonoids and phenolic compounds associated with

1034   plant defense response against several biotic and abiotic stresses (Kim et al. 2007).

1035   This implies that the exogenous application of PGRs mitigate drought stress and improve

1036   soybean tolerance to drought stress through increased water use potential, leaf water potential,

1037 nitrate reductase activity, chlorophyll contents, and photosynthesis (Zhang et al. 2007),

1038 contributing to increased translocation of ^{14}C assimilates, dry weight accumulation, and high leaf

1039 area (Mohamed & Latif 2017). This significantly increased the yield-related parameters and

1040 subsequently improved the overall seed yield of soybean, indicating the ability of PGRs to

1041 stimulate soybean growth and improve yield even under drought stress.

1042 3.5.4 Waterlogging

1043 Waterlogging occurs when plant roots are surrounded by water or the shoots are partially or

1044 entirely covered with water (Sullivan et al. 2001). Waterlogging is the most frequent flooding

1045 condition, characterized by excessive rainfall and/or the overspill of rivers (Kim et al. 2015) and

1046 it is one of the limiting factors in global soybean (a flood-sensitive crop) cultivation.

1047 Waterlogging negatively influences many physiological processes in plants by reducing

1048 photosynthesis, nutrient uptake, and causes hormonal imbalance that negatively affects the

1049 growth and yield of soybean (Kim et al. 2015; Valliyodan et al. 2017). For example, substantial

1050 yield loss was observed in soybean under severe waterlogging stress during the vegetative (17 to

1051 43%; Reyna et al. 2003) and reproductive (50 to 56%; Scott et al. 1990) growth stages. Similarly,

1052 soybean plants exposed to waterlogging stress recorded a 17% and 57% yield loss at the

1053 vegetative and reproductive stages respectively, compared to non-stressed plants (Nguyen et al.

1054 2012). A recent report by Rhine et al. (2010) suggested a 39% yield loss in waterlogging-tolerant

1055 soybean varieties as against the 77% yield loss in susceptible varieties under severe waterlogging

1056 conditions.

1057 Plants develop many strategies to mitigate the adverse effects of waterlogging stress and improve

1058 their tolerance. Among them, is the escape strategy which allows gaseous exchange between

1059 cells and their environment due to the changes that occur in both the anatomical and

1060   morphological structures of the plant including adventitious root formation, shoot elongation,

1061   and aerenchyma cell development (Bailey-Serres & Voesenek 2008). Recently, several studies

1062   have reported the use of exogenous plant growth regulators as an effective alternative to mitigate

1063   the deleterious effects of waterlogging stress in plants. Kim et al. (2015) indicated that the

1064   application of GA, and ETP improved tolerance to waterlogging stress than in control plants.

1065   Treatments 50 μM and 100 μM ETP had the best effect, recording the highest GA concentrations

1066   even after short-term stress. The results revealed that GA- and ETP-treated soybean plants

1067   developed an escape strategy under waterlogging by the hyper-elongation of the shoot which

1068   increased the overall plant height. This then confirms that the accumulation and fluctuations in

1069   the endogenous GA levels induce the escape strategy. In another study, Kim et al. (2018)

1070   reported the ability of ETP to ameliorate waterlogging stress in soybean plants. This ameliorative

1071   effect of ETP was due to its ability to induce the overexpression of antioxidant enzyme activity.

1072   Overall, this could promote growth and improve soybean productivity under waterlogging stress.

1073   Root length is among the key response indicators to waterlogging stress in plants. Tolerance of

1074   soybean plants to waterlogging stress correlates sturdily to the overall root growth (length,

1075   surface area, and dry weight; Sallam & Scott 1987). Recently, Kim et al. (2018) documented that

1076   waterlogging stress can impede root growth in soybean by reducing the root size and RSA.

1077   However, the exogenous application of ETP to soybean plants subjected to waterlogging stress

1078   increased the root size and RSA which promoted root growth and nutrient (K and P) uptake.

1079   ABA is a key hormone in water stress response. According to recent research, endogenous ABA

1080   contributes to the development of aerenchyma cells in root tips during waterlogging to facilitate

1081   the absorption and transport of oxygen (Shimamura et al. 2014). Endogenous ABA decreases in

1082   response to waterlogging stress to keep the stomata open, providing greater surface area for

1083 oxygen entry and removal of excess water (Shimamura et al. 2014). Increasing research suggests

1084 that the downregulation of endogenous ABA suppresses suberin biosynthesis which keeps the

1085 root cell unsuberized for aerenchyma cell development in soybean. Similarly, Kim et al. (2015)

1086 observed a significant decrease in ABA contents and well-developed aerenchyma cells in

1087 waterlogging tolerant soybean variety compared to non-tolerant variety and control. This

1088 suggests the crucial role of ABA in regulating soybean tolerance to waterlogging stress, thus

1089 promoting growth and productivity. In conclusion, the exogenous application of plant growth

1090 regulators can mitigate waterlogging stress in soybean by improving waterlogging tolerance

1091 through the development of the escape strategy, increased accumulation of endogenous GAs,

1092 induced antioxidant enzyme activity, and increased root growth which promoted nutrient uptake.

1093 This in effect promoted the overall growth and productivity of soybean under waterlogging

1094 stress. However, the significant internode growth observed in the GA- and ETP-treated soybean

1095 plants subjected the plants to lodging (Seo et al. 2017). It can, therefore, be proposed that the use

1096 of exogenous GA and ETP may be ineffective for the commercial production of soybean.

1097 **4.0 Conclusion**

1098 PGRs are commonly applied in agriculture to improve germination, seedling establishment,

1099 growth, and development as well as yield even under unfavorable environmental and soil

1100 conditions. At low concentrations, PGRs control the structure and function of the cell, cell

1101 division and expansion together with the regulation of environmental stresses. Application of

1102 PGRs directly to the leaves, shoots, buds, roots, and flowers protects plants from biotic and

1103 abiotic stresses, enhances water use efficiency, breaks dormancy, and improves drought

1104 tolerance among others. PGRs applied at the proper period of growth and appropriate

1105 concentrations influence the yield and yield components of soybean (as outlined in Figure 3).

1106   Several studies only concentrated on the essential roles played by PGRs on the various

1107   physiological, morphological, and biochemical properties together with yield and quality traits of

1108   soybean. Nevertheless, studies on the use of PGRs to enhance the growth and development of the

1109   anatomical structures that contribute to the entire well-being of the plant and consequently its

1110   yield is inadequate. Therefore, further studies are needed to bridge this aforementioned gap.

1111   Future works could be focused on the effects of plant growth regulators on these structures to

1112   increase our understanding of the mechanisms employed by the various growth regulators to

1113   influence growth in these plant parts and increase productivity. All in all, one could judge that

1114   PGRs do not only promote the growth and development of the soybean plant but also increase

1115   productivity. An illustration of the different growth stages of the soybean plant, from

1116   germination to maturity is presented in figure 4.

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Nutritional value of soybean per 100g of dry matter.

1 **Growth Regulators Promote Soybean Productivity: A Review**

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3 Zheng[1,2]*, and Hongbo Zhu[1]*

4 **Table 1:**

5 **Nutritional value of soybean per 100 g of dry matter.** *Source* adapted from (Lokuruka 2010)

Nutrient		Amount	Unit
Energy		1,866 (446)	kJ (kcal)
Carbohydrates		30.16	g
	Sugars	7.33	g
	Dietary fiber	9.3	g
Fat		19.94	g
	Saturated	2.884	g
	Monounsaturated	4.404	g
	Polyunsaturated	11.255	g
	omega 3	1.330	g
	omega 6	9.925	g
Protein		36.49	g
	Tryptophan	0.591	g
	Threonine	1.766	g
	Isoleucine	1.971	g
	Leucine	3.309	g
	Lysine	2.706	g
	Methionine	0.547	g
	Cystine	0.655	g
	Phenylalanine	2.122	g
	Tyrosine	1.539	g
	Valine	2.029	g
	Arginine	3.153	g

	Histidine	1.097	g
	Alanine	1.915	g
	Aspartic acid	5.112	g
	Glutamic acid	7.874	g
	Glycine	1.880	g
	Proline	2.379	g
	Serine	2.357	g
	Vitamin A equivalent	1	µg
	Thiamine (B1)	0.874	mg
	Riboflavin (B2)	0.87	mg
	Niacin (B3)	1.623	mg
	Pantothenic acid (B5)	0.793	mg
Vitamins	Vitamin B6	0.377	mg
	Folate (B9)	375	µg
	Choline	115.9	mg
	Vitamin C	6.0	mg
	Vitamin E	0.85	mg
	Vitamin K	47	µg
	Calcium	277	mg
	Copper	1.658	mg
	Iron	15.7	mg
	Magnesium	280	mg
Minerals	Manganese	2.517	mg
	Phosphorus	704	mg
	Potassium	1797	mg
	Sodium	2	mg
	Zinc	4.89	mg
Water		8.45	g

6   * KJ = Kilo-joules, kcal = kilocalorie, g = grams, mg = milligrams, µg = micrograms.

Figure 1

Action of PGRs in regulating growth and development of the soybean plant. *Source* modified from Nadeem et al. (2019).
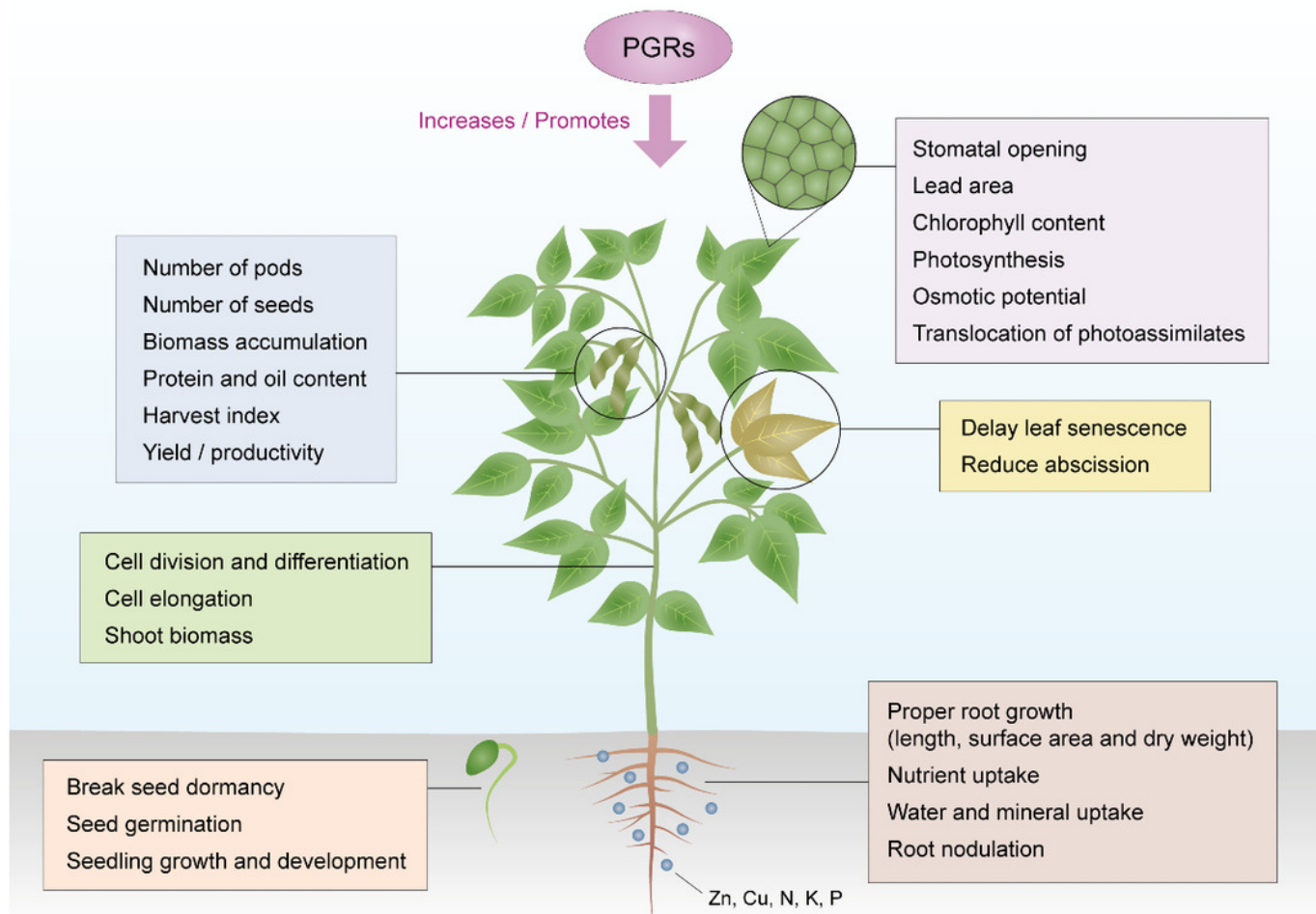
Figure 2

The main antioxidant defense system and the various reactions involved in scavenging ROS from cells.

CAT: catalase, APX: ascorbate peroxidase, POD: peroxidase activity, SOD: superoxide dismutase, GR: glutathione reductase, GSH: glutathione, NADPH: nicotinamide adenine dinucleotide phosphate, GSSG: glutathione disulfide, GPX: glutathione peroxidase, GST: glutathione S-transferase, ASC/AsA: ascorbate, DHA: dehydroascorbate, $^1O_2$: singlet oxygen, H_2O: water, O_2: molecular oxygen, $OH^•$: hydroxyl radical, H_2O_2: hydrogen peroxide, and $O_2^{•-}$: superoxide radical. In the long process of natural evolution, plants themselves have established a set of extremely complex antioxidant defense mechanisms to avoid or alleviate oxidative damage. As the main defense system against ROS in vivo, the antioxidant defense consisting of a systematic network of both enzymatic and non-enzymatic antioxidants work coordinately to scavenge free radicals from cells. SOD enzyme catalyzes the decomposition of $O_2^{•-}$ into H_2O_2 which may react with membrane lipids to undergo a chain of reactions and further be converted to H_2O and O_2 by various antioxidants such as CAT, GSH, GSSG, GPX, AsA, DHA, and GR. The $OH^•$ generated by H_2O_2 is further scavenged by GSTs. The non-enzymatic antioxidant system, on the other hand, does not directly protect against ROS but works in synergy with the endogenous enzymatic antioxidant system to scavenge free radicals by augmenting their functions.

Enzymatic Antioxidants

SOD $O_2^{\cdot-} + O_2^{\cdot-} + 2H^+ \rightarrow 2H_2O_2 + O_2$

CAT $2H_2O_2 \rightarrow O_2 + 2H_2O$

APX $H_2O_2 + AsA \rightarrow 2H_2O + DHA$

GPX $DHA \rightarrow 2H_2O + GSSG$

GR $GSSG + NADPH \rightarrow 2GSH + NADP^+$

POD $H_2O_2 + GSH \rightarrow H_2O + GSSG$

Non-Enzymatic Antioxidants

AsA scavenge $O_2^{\cdot-}$, OH·, and $^1O_2$ and reduce H_2O_2 to H_2O via the APX reaction

GSH substrate for PODs, GSTs and GR, scavenger of $^1O_2$, H_2O_2 and OH·, acts in regenerating AsA via the AsA-GSH cycle
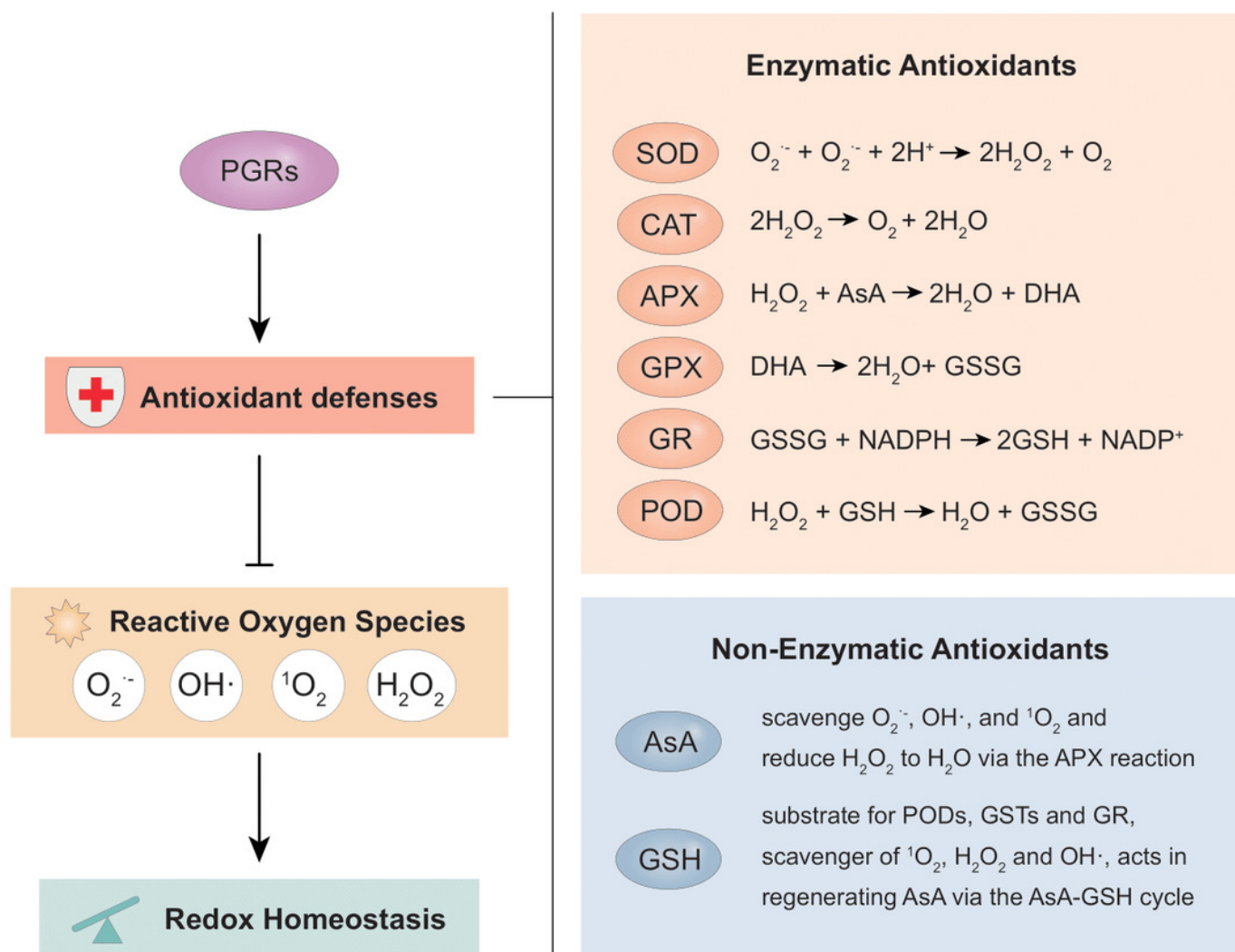
Figure 3

Summary of the effects of plant growth regulators on the growth and development of soybean.
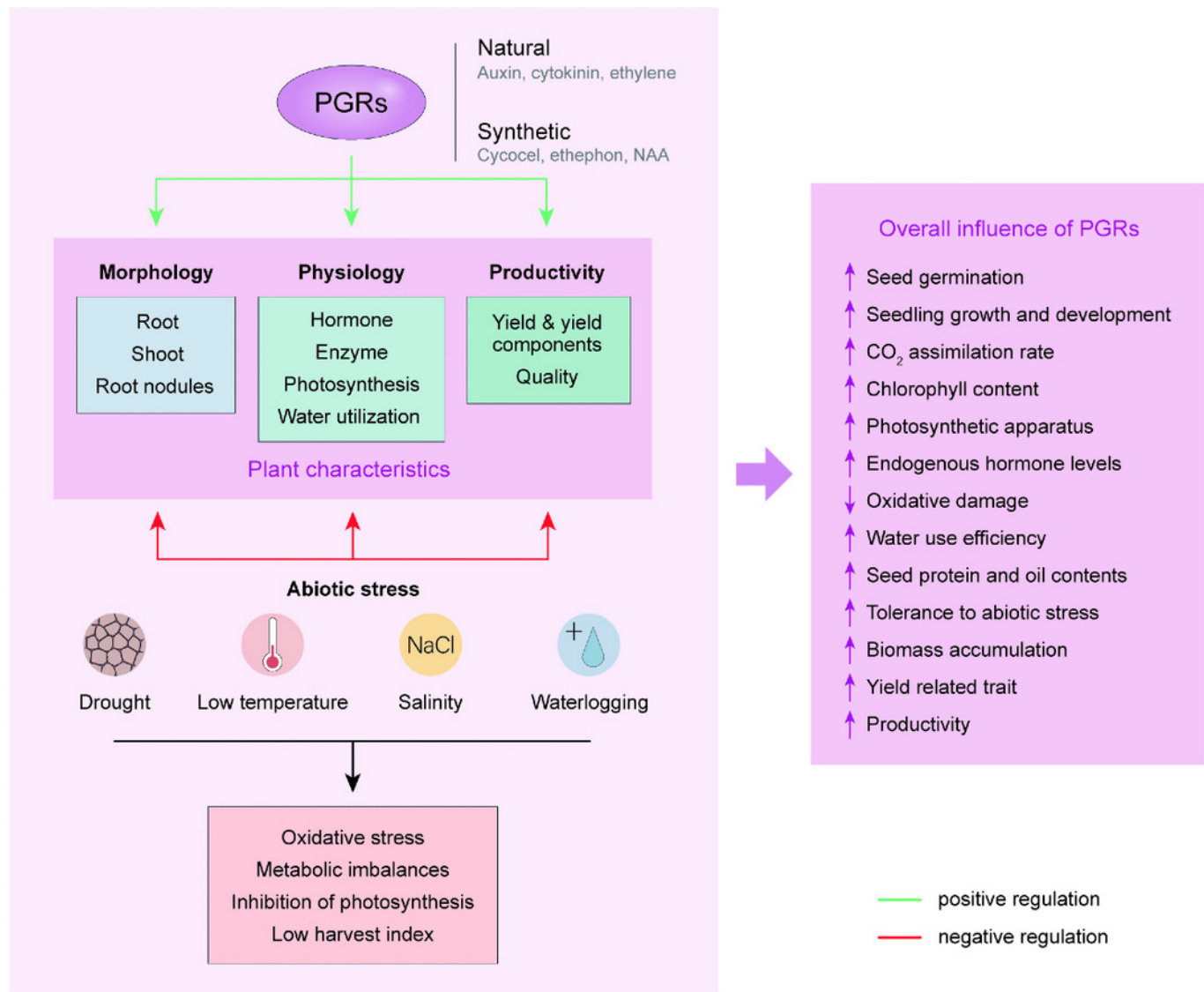
Figure 4

Stages of soybean growth from germination to maturity. *Source* modified from Hodgson et al. (2012).

Vegetative stage

cotyledons
emergered

unifoliolate leaves
unrolled so leaf
edges not touching

first trifoliolate
leaves unrolled

second trifoliolate
leaves unrolled

third to nth trifoliolate
leaves unrolled

VE — Emergence

VC — Cotyledon

V1 — First Trifoliolate

V2 — Second Trifoliolate

V3 –V(n) — Stages V3 – V(n)

Reproductive stage

open flower
at any node
on main stem

open flower
at one of the
two u.n.
on main stem

pods <5/16 in
(5 mm) long
at four u.n.

pods <3/4 in
(2 cm) long
at four u.n.

seed is 1/8 in
(3 mm) long
at one of four u.n.

top view

side view

green seed
that fills pod capacity
at one of four u.n.

top view

side view

one pod
on the main stem
has reached mature
pod color

top view

side view

95% of pods
have reached
mature
pod color

R1 — Beginning Flowering

R2 — Full Bloom

R3 — Beginning Pod

R4 — Full Pod

R5 — Beginning Seed

R6 — Full Seed

R7 — Beginning Maturity

R8 — Full Maturity

u.n. : uppermost nodes