Journal of Medicinal and Industrial Plants (2025) 3 (1): 1- 15
ISSN: 2959 – 121X
DOI: https://doi.org/10.32894/MEDIP.25.3.1

Increased CO2 in the environment and its effect on hormonal imbalance in plants: A Review Article.

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Annotation
Maintaining hormonal balance in plants is a significant challenge, and it becomes even more critical under environmental stress conditions, which lead to plant stress, whether biotic or abiotic. This is because plant hormones, in conjunction with other molecular signals, determine the direction of growth (increase or decrease), its extent (cell number and size), its nature (vegetative or reproductive), and the plant's response to the surrounding environmental conditions. This makes hormonal imbalance a critical existential challenge for plants. The increase in CO2 has multiple effects on hormonal balance and, consequently, on plant growth and productivity. It boosts hormones that promote vegetative growth while reducing inhibitors, stimulating important processes such as chlorophyll production and preservation from degradation, enhancing photosynthesis efficiency, improving nutrient absorption from the soil, maintaining water balance, and increasing the efficiency of transport processes within the plant. This results in an increase in the biomass produced per unit area, which is beneficial. However, it could also lead to excessive vegetative growth, shading of lower leaves, and a delay in reaching the reproductive growth stage, potentially reducing the harvest index despite an increase in total dry matter. Although increased CO2 enhances the plant's tolerance to heat stress, elevated temperatures do not only represent heat stress but also water stress due to rapid evaporation. This can lead to soil salinization because salt accumulation causes ionic and oxidative stress. This imbalance in hormonal, nutritional, and oxidative systems is difficult to predict with precision, but it generally represents a disruption in the system that hinders the plant's healthy growth. Additionally, it increases the plant's susceptibility to serious fungal diseases. Therefore, addressing the increase in CO2 using all available means is a necessity, not a luxury. Permanent changes in the climate may occur that cannot be reversed, such as large floods, hurricanes, wildfires, droughts, dust storms, and the resulting famines and compounded disasters.

KEY WORDS: Abiotic stress, plant hormones, plant growth under global warming.

Received: 30/12/2024 ; **Accepted**: 30/01/2025 ; **Available online:** 31/03/2025

زيادة ثاني أكسيد الكربون في البيئة وتأثيره على اختلال التوازن الهرموني في النباتات: مقالة مراجعة.

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تعليق توضيحي:
يُعتبر الحفاظ على التوازن الهرموني في النباتات تحديًا كبيرًا، ويصبح أكثر أهمية في ظل ظروف الإجهاد البيئي، سواء كان حيويًا (**biotic**) أو غير حيوي (**abiotic**). يعود ذلك إلى أن الهرمونات النباتية، بالتعاون مع إشارات جزيئية أخرى، تحدد اتجاه النمو (زيادة أو نقصان)، ومداه (عدد وحجم الخلايا)، وطبيعته (نمو خضري أو تكاثري)، واستجابة النبات للظروف البيئية المحيطة. مما يجعل اختلال التوازن الهرموني تحديًا وجوديًا بالغ الأهمية للنباتات.
تؤدي زيادة ثاني أكسيد الكربون إلى تأثيرات متعددة على التوازن الهرموني، وبالتالي على نمو النبات وإنتاجيته. حيث تُعزّز الهرمونات التي تشجع على النمو الخضري وتقلل من مثبطات النمو، مما يحفز عمليات هامة مثل إنتاج الكلوروفيل والحفاظ

عليه من التحلل، وزيادة كفاءة التمثيل الضوئي، وتحسين امتصاص المغذيات من التربة، والحفاظ على توازن الماء، وزيادة كفاءة عمليات النقل داخل النبات. يؤدي ذلك إلى زيادة في الكتلة الحيوية المنتجة لكل وحدة مساحة، وهو أمر مفيد. ومع ذلك، قد يؤدي أيضًا إلى نمو خضري مفرط، ما يسبب تظليل الأوراق السفلى وتأخر الوصول إلى مرحلة النمو التكاثري، مما قد يقلل من مؤشر الحصاد رغم زيادة المادة الجافة الإجمالية. وعلى الرغم من أن زيادة ثاني أكسيد الكربون تعزز تحمل النبات للإجهاد الحراري، إلا أن ارتفاع درجات الحرارة لا يمثل فقط إجهادًا حراريًا بل يؤدي أيضًا إلى إجهاد مائي نتيجة التبخر السريع. وقد يسبب ذلك تملح التربة بسبب تراكم الأملاح، مما يؤدي إلى إجهاد أيوني وإجهاد تأكسدي. يصعب التنبؤ بهذا الاختلال في الأنظمة الهرمونية والغذائية والتأكسدية بدقة، ولكنه يمثل عمومًا اضطرابًا يعوق النمو الصحي للنبات. بالإضافة إلى ذلك، يزيد من قابلية النبات للإصابة بأمراض فطرية خطيرة. لذلك، فإن معالجة مشكلة زيادة ثاني أكسيد الكربون باستخدام جميع الوسائل المتاحة ضرورة وليست رفاهية.

الكلمات المفتاحية: الإجهاد غير الحيوي، هرمونات النبات، نمو النبات في ظل الاحتباس الحراري.

INTRODUCTION

Plant hormones play a crucial role in regulating developmental events within the apical meristem, such as cell division, elongation, and protein synthesis (D'Agostino and Kieber, 1999). They activate, modify, or inhibit growth in a balanced way according to the surrounding environmental conditions. Plant hormones regulate key processes like seed germination, vegetative and reproductive growth, and yield formation. These hormones adjust plant responses to environmental changes, ensuring balance during growth stages, yield formation, and physiological maturity-form an organized sequence of stimulation, inhibition, and precise hormonal balance. These growth regulations are carried out by hormones such as auxins, gibberellins, cytokinins, ABA, salicylic acid, jasmonates (JAs), brassinosteroids (BRs) (Kosakivska et al., 2022) Plant hormones are very important endogenous compounds that help regulate the physiology and Molecular responses of plants that are essential for the growth and development of plants that can survive in harsh environments and to increase Tolerance to environmental stress (Ali et al., 2024) Disruption of hormonal balance in plants is how plants cope with stress, which affects physiological and biochemical processes This ultimately results in a decrease in productivity. Since the Industrial Revolution, levels of CO_2 in the atmosphere have increased significantly due to human activities. This wind is responsible for climate change (Droulia and Charalampopoulos, 2021). Increased CO_2 levels and global warming have a direct effect on plants (Gamage et al., 2018). Climate change significantly amplifies the frequency of extreme weather events, such as heatwaves, droughts, floods, salinity, food shortages, and other events that ultimately lead to rising temperatures, making global warming an unavoidable phenomenon. As a result, the world now faces a critical challenge in the form of climate change, characterized by major and permanent shifts in weather patterns. Significant climate changes are expected due to global warming, which may be either predictable or unpredictable, as the impacts of this phenomenon are numerous and interconnected, making it difficult to determine a definitive direction. For example, increased CO_2 levels may enhance the photosynthesis process, particularly in C3 plants, leading to an increase in biomass. However, the rise in CO2 also exacerbates the greenhouse effect, which stresses plants and increases photorespiration, leading to a loss in dry matter production, potentially as much as 25%. Heat stress causes stomata's closure to maintain plant tissue's water balance. On the other hand, an increase in its levels enables plants to tolerate heat stress. Therefore, it is difficult to predict which physiological process will be most adversely affected by climate change, although the overall impact is generally negative. Climate change-related stresses are expected to negatively influence plant productivity in the coming decades. This change may lead to significant disruptions in future food security, especially in poor countries, where crops are exposed to both biotic and abiotic stresses. Such changes affect plant hormones, reactive oxygen signaling, secondary metabolic pathways, and plant defense responses.

The indirect effect of increased CO_2 on hormonal balance

Elevated atmospheric CO_2 concentrations directly or indirectly influence various plant processes, including physiological functions, metabolism, gene expression, and productivity (Ahammed et al., 2020; Zhou et al., 2019a; Zinta et al., 2018). The indirect effect of CO_2 on plant hormones is mediated through its impact on enhancing photosynthetic rates. This growth provides the structural elements necessary for further cell division. Therefore, it expands tissues that require stimulation of plant hormones that promote growth. and inhibit growth inhibitors In addition to providing the necessary precursors for hormone synthesis Increases the activity of the tissues responsible for producing these hormones. These active tissues include the meristem zones in shoots, root tips, and seed embryos, and other positions that is considered a hub for hormone synthesis. In addition, increased CO2 concentrations in the plant environment may interfere with the selectivity of the hormone transport system by regulating the type and amount of Hormone transport Hormonal balance can be altered (Wei et al., 2013).

The direct effect of elevated CO2 levels on hormonal balance

Plant hormones are important requirements for adjusting plant growth to different levels of CO2 in the environment (Gupta et al., 2005; Teng et al., 2006; Wei et al. 2013). Higher CO2 levels boost growth hormones like auxins and gibberellins, promoting cell division and increasing biomass. (Gamage et al., 2018) Hormone metabolism plays an important role in growth and development. of plants (Gamage et al., 2018; Gangappa and Botto, 2016; Geiss et al., 2018) because changes in hormone activity are directly linked to biomass, with increased growth under high CO2 levels (Gamage et al., 2018) various plant responses Abscisic acid (ABA) has been specifically described to coordinate atmospheric changes including carbon dioxide and Other greenhouse gases Not limited to As an example of Teng et al.'s research, Arabidopsis leaves grown at high carbon dioxide concentrations have higher amounts of auxin. (indole-3-acetic acid, IAA), gibberellin (gibberellic acid, GA3) and cytokinin in higher amounts than leaves grown at Low carbon dioxide 2 (Catovsky et al. 2006). An increase of transcription level for the genes involving in synthesis and transport of auxins, cytokinins and gibberellins may explain this (Wei et al., 2013). In particular, higher atmospheric CO_2 may relieve detriments to plants from heat stress that is frequently found with increasedCO_2. It mitigates this through multiple mechanisms such as stomatal regulation of stomata movement, osmotic adjustments via modification in cell membrane permeability, and an increase in water use efficiency (Li et al., 2019; Zhang et al., 2019). Plant responses to elevated CO_2 involve multiple signaling pathways most of which are dictated by plant hormones concerning pathogen resistance. More precisely, elevated CO_2 induces de novo salicylic acid (SA) biosynthesis and represses jasmonic acid (JA) pathways. This hormone modulation induces SA signaling pathway and represses the JA cascade, thus improving resistance to biotrophic and hemibiotrophic pathogens. Nonetheless, the change in plant exudation pattern will both favor the establishment and virulence of necrotrophic fungal pathogens. The response of plants to previous crop rotations has varied widely across species (Asim et al, 2019) and growth conditions (Li and Ahammed, 2023), photoperiods (Barya et al, 2020), and fertilizer management or cropping systems may even produce a different recommendation. (Platonova et al., 2016). These observations imply that the predicted rise in CO_2 may lead to pronounced crop losses through a higher incidence of fungal pathogens.

Enhancement of CO_2 concentration has been reported to decrease attack rates and damage by Tobacco Mosaic Virus (TMV) and Pseudomonas syringae on plants. Nevertheless, it enhanced the susceptibility of plants to Botrytis cinerea, a cosmopolite fungus and one of the most important threats to crop production worldwide (Zhang et al., 2015).

Auxins (IAA)

Auxins are one of the most well-known plant hormones and were the first ever discovered. They control root and branch development and general growth, eliciting both synergistic or antagonistic responses with cytokinins in different cellular and physiological functions (Tromas et al., 2009; Jurado et al., 2010), including the cell cycle, cell elongation, branching and apical dominance, subliminal leaf levels, and embryonic seed maturation. Auxins play diverse roles in plants, and one of its significant functions is lateral root development. These roots are especially significant for the plants as they control root system architecture and affect its gainfulness in nourishing as well as water uptake (Sabagh et al., 2022).

The distribution, balance and metabolism of auxins are influenced by abiotic environmental stresses within the cellular environment. These alterations in auxin distribution during the stress conditions are explained by two proposed mechanisms. The first mechanism concerns changes in gene expression, and the second is based on the notion that a phenolic compound that accumulates during stress reduces polar auxin transport (Kovtun et al. 2000; Potters et al. 2009). Auxins are of particular importance in plants' responses to environmental stress since they regulate growth adjustment. As such stresses are associated with alterations in auxin concentrations; they can then also trig error plasticity response by distorting plant growth and development resulting in morphological deviations. Such morphological switches in response to stress are adaptive responses to minimize or avert the ill effects that have been discussed above (Potters et al., 2009).

Tomato shoots produce auxin (IAA) in response to elevated CO_2 levels, which could further promote the polar auxin transport (Zhou et al., 2019a). The stimulus from high glucose and sucrose could lead to increased biosynthesis of auxin in the plants, a possible effect of high CO_2 in the atmosphere. Of these, sucrose has a more pronounced effect on auxin biosynthesis (Sairanen et al., 2012). As an illustration, data by Teng et al. (2006) isolated the effect of increased CO_2 on plant hormones in Arabidopsis thaliana and found appreciably higher levels or concentrations of plant hormones including [[auxin]] (Indole-3-acetic acid, IAA), gibberellic acid, and cytokinins such as zeatin riboside, dihydrozeatin riboside, dihydrozeatin riboside, and isopentenyl adenosine. These cytokinins play vital roles in regulating various growth and developmental processes in plants.

Gibberellins (GAs)

Gibberellins represent a large group of plant hormones that significantly influence various physiological functions. They serve as key regulators of reproductive organ formation, fruit development, ripening, and seed germination (Plackett & Wilson, 2016). Gibberellins can either promote or inhibit seed germination under high-temperature conditions (Urbanová & Leubner-Metzger, 2016). They are also known to mediate numerous physiological and developmental processes in plants (Hedden & Phillips, 2000). To date, 136 types of gibberellins have been identified across 128 plant species, though only a few are biologically active, including GA_1, GA_3, GA_4, and GA_7. Interestingly, the production of GAs is not limited to plants; various bacterial species, such as Bacillus pumilus and B. licheniformis, as well as some fungi, are also capable of producing these hormones (Gutiérrez-Mañero et al., 2001). Biologically active gibberellins play a critical role in stimulating seed germination, stem elongation, flowering, and fruit formation by promoting the degradation of DELLA proteins (Gao et al., 2017). These proteins are key components of hormone signaling pathways in plants (Davière and Achard, 2015). Gasparini et al. (2019) reported that elevated CO_2 levels promote plant growth only when gibberellin biosynthesis becomes unnecessary. Additionally, GAs regulate plant adaptation to biotic and abiotic stresses (Davière and Achard, 2015). High concentrations of CO_2 act as a signal enabling higher growth rates in plants experiencing low GA_3 levels, as CO_2 independently stimulates biomass accumulation by regulating the expression of growth-related genes (Ribeiro et al., 2013).

Cytokinins

Cytokinins play a variety of roles in plants. Including increasing the amount of chlorophyll (Dobránszki & Drienyovszki, 2014) and stimulating cell division. The diverse roles of cytokinins are fundamentally related to their complex interactions with other phytohormones (Gan et al., 2022). A notable example is their dual relationship with auxin. which act synergistically in cell division and maintain the opposing role of controlling the elite. This pattern of hormonal crosstalk represents a broad pattern. of the behavior of plant hormones Their interactions may be additive or antagonistic depending on the physiological context...

Cytokinins have a profound impact on various physiological biochemical pathways. Including the synthesis and maintenance of chlorophyll. photosynthesis migration and regulation of enzymes (Sosnowski et al., 2023). Their efficiency is influenced by external factors. Especially hormonal balance. and the duration of photoperiod, light conditions, non-living things Stress conditions, nutrient conditions and are adjusted by environmental factors such as the developmental stage of plant tissues and living things.

Cytokinin's anti-aging properties are expressed through its ability to maintain nitrogen and protein concentrations. especially the level of the enzyme Rubisco, which helps maintain photosynthesis efficiency (Jordi et al., 2000). This anti-aging effect extends to mature plant tissues. possibility (Hönig et al., 2018). Cytokinin also facilitates the redistribution of nitrogen from old, light-limited leaves to light-exposed leaves (Boonman et al., 2007). Positively, the nitrogen content in leaves and the abundance of photosynthetic proteins are reduced by nitrogen acquisition. of genes involved in determination and process is achieved through transcriptional regulation (Ruffel et al., 2011) .

The more desirable root development determined underneath accelerated CO_2 conditions is mediated via modulation of phytohormone homeostasis, especially through augmented indole-three-acetic acid (IAA) and isopentenyl adenosine (iPA) concentrations. This regulation occurs through transcriptional control of auxin and cytokinin biosynthetic pathways, coupled with downregulation of cytokinin catabolic genes (Fan et al., 2022). The CO_2-mediated growth stimulation encompasses multiple physiological mechanisms, including enhanced availability of cellular building blocks essential for tissue morphogenesis. Furthermore, this response involves a recalibration of hormonal equilibrium that promotes vegetative development through heightened activity of auxin and cytokinin, two primary phytohormones governing cellular division processes.

Ethylene (ET)

Although it belongs to the plant hormones family, ethylene is the sole gaseous stimuli between this one. The role of it is important in many physiological processes ranging from flowering, fruit ripening and overcome plant environmental stresses such as extreme temperature, drought, salinity, heavy metals and flooding stress (Awan et al., 2017). Ethylene concentrations were reported to increase in response to cold and freezing stress in Arabidopsis and Medicago truncatula (Shi et al., 2012; Zhao et al., 2014). Ethylene enhances the sodium-to-potassium ratio as well as ROS between during salt stress leading to high level of ethylene induction thus, HS (Yang et al., 2017). In addition, ethylene has an important role in the natural responses of plants to ultraviolet radiation, nutrient deficiencies, pathogen attack and mechanical injury. It is synthesized and accumulated in the tissues responding at a site of damage or to mechanical wounds (Kendrick and Chang, 2008) .

Pan et al. His experience was supported by the findings of (2019) who reported, plants under elevated CO_2 conditions showed increased ethylene production. It was due to the accumulation of 1-aminocyclopropane-1-carboxylic acid oxidase (ACO), which catalyzes the conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene. It shows that high CO_2 in particular via boosting ethylene whilst underneath stress can also offer relative thermo-, salinity, drought, heavy metals, nutrient deficiency and so on, mechanical damage and pathogen tolerance. Elevated CO_2 situations, while generally beneficial for plant boom, show off physiological thresholds past which strain responses emerge as glaring. This is especially applicable when multiplied CO_2 coincides with thermal strain, potentially imposing compounded constraints on plant growth and developmental techniques. Research conducted by way of Seneweera et al. (2003) tested improved ethylene biosynthesis in flora grown below extended CO_2 conditions compared to the ones underneath ambient CO_2 tiers. This vegetation showcases augmented capacity for converting 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene, mediated by way of elevated expression of ACC oxidase. The accumulation of this enzyme demonstrates an immediate correlation with CO_2 concentrations, therefore affecting ethylene manufacturing tiers (Finlayson & Reid, 1996) .

In rice flowers, the elevation of ethylene production in response to multiplied CO_2 plays an important role in promoting increase, especially through the enhancement of tiller initiation and proliferation, potentially leading to advanced grain yield (Seneweera et al., 2003). Additionally, Ahmed et al. (2021) suggest that ethylene serves as a number one hormonal regulator in conferring thermotolerance below multiplied CO_2 conditions.

Abscisic Acid (ABA)

The phytohormone abscisic acid (ABA), first identified within the early 1960s as a regulator of seed dormancy (Cornforth et al., 1965), has given that been recognized for its multifaceted roles in plant boom, improvement, and strain reaction (Guschina et al., 2002; Iqbal, 2015). As a key mediator of stomatal law and water balance, ABA performs a crucial role in retaining plant water members of the family. Under water-deficit conditions, ABA is synthesized in root tissues and sooner or later translocated through the xylem to the leaves, in which it accumulates. In protecting cells, ABA regulates turgor stress and potassium homeostasis, main to stomatal closure and thereby decreasing water loss (Awan et al., 2017) .

ABA’s characterization as the "stress hormone" arises from its accumulation in response to both biotic and abiotic stressors. Beyond its function in regulating transpiration via stomatal closure, ABA additionally contributes to plant protection via restricting pathogenic invasion. It promotes the synthesis of strain-defensive compounds, including proline, sphingolipids, and polyamines. Additionally, ABA interacts with other phytohormones, especially salicylic acid (SA) and methyl jasmonate (MJ), to enhance plant resilience and adaptability to numerous environmental stressors (Bharath et al., 2021).

ABA orchestrates a comprehensive stress reaction via its signaling pathways and hormonal crosstalk (He et al., 2018). Under abiotic strain conditions, ABA turns on various biochemical protection mechanisms, consisting of the law of biosynthetic pathways, proline metabolism, antioxidant structures, and reactive oxygen species (ROS) detoxification enzymes. It also stimulates the synthesis of heat shock proteins and the stabilization of cuticular wax, thereby enhancing stress tolerance (Chen et al., 2013; Lee and Suh, 2015; Hoque et al., 2016; Huang et al., 2016; Yin et al., 2018; Singhal et al., 2021).

Finkelstein (2013) highlights the crucial role of ABA in mediating environmental pressure responses, inclusive of stomatal law and the postponement of senescence. Interestingly, increased atmospheric CO_2 concentrations were proven to significantly reduce endogenous ABA tiers, indicating complicated interactions among environmental elements and hormonal regulation.

Teng et al. (2006) propose that these phenomena can be related to delayed senescence, with alterations in ABA metabolism probably influencing plant boom and improvement beneath multiplied CO_2 conditions. As ABA is a key regulator of stomatal conductance, changes in its dynamics in response to expanded CO_2 may also affect other physiological procedures, together with water use efficiency (Chater et al., 2015).

The reduction in ABA accumulation below improved CO_2 tiers is attributed to the downregulation of genes concerned in ABA synthesis, coupled with an expanded degradation method (Teng et al., 2006; Wei et al., 2013). This decrease in ABA may, in turn, delay plant senescence under growing CO_2 concentrations (Fang et al., 2019). However, this sort of reduction also diminishes the benefits related to keeping optimum ABA levels, specifically in response to diverse abiotic stresses. Consequently, the reduced ABA levels ought to compromise vital procedures, including drought tolerance and normal physiological functions like fruit ripening. These benefits are usually performed whilst ABA is carried out at the most suitable concentrations and inside the correct timeframes. However, multiplied CO_2 tiers result in a discount of ABA, which can disrupt these methods and impair the plant's capacity to efficaciously adapt to and resist abiotic stresses. This decline in ABA may also hinder essential physiological responses, in the long run compromising the plant's resilience and overall pressure tolerance.

Salicylic Acid (SA) and Jasmonic Acid (JA)

Salicylic acid (SA) is an essential plant hormone that now not only regulates components of normal growth but also environmental strain responses and plant defense against pathogens. It is a secondary metabolite of plant, microorganism and fungal starting place that is a shikimate pathway derivative (Mishra and Baek, 2021). SA interacts with other plant hormones which include jasmonic acid (JA), ethylene (ET), abscisic acid (ABA), and others to carry out vital roles in plant responses to environmental situations.

Signaling responses mediated via SA are regulated through a complex interaction among gene, proteins, and transcription factors (Sapna et al., 2024). SA performs an essential role in regulating the manufacturing and scavenging of reactive oxygen species (ROS), key element in plant defense responses. ROS-mediated mechanisms include the induction of hypersensitive response (HR) at the site of pathogen infection that restricts local spread of pathogens and also activates both local and systemic defense pathways (Noman et al., 2020).

Hayat et al. The most essential physiological functions of salicylic acid (SA) in plants are summarized by (2007) including enhancement of mineral uptake from soil along with growth, the production of chlorophyll and carotenoid, improvement of photosynthetic efficiency, flowering induction, ethylene production and hormonal balance stomatal regulation as well as increasing various environmental stresses. SA also has the potential to enhance biomass production and stimulate plant innate immune responses, such as resistance against pathogens

The biosynthesis of jasmonates (JAs) take place chiefly in two plant organs: leaves and roots, while the main subcellular sites are chloroplasts and peroxisomes (Cheong and Choi, 2003). Jasmonates are a major class of phenolic compounds produced by plants that are involved in hormonal equilibrium and environmental responses. They are helpful in minimizing the adverse effects of salinity when sprayed on foliage (Horváth et al., 2007) and play an important role in conferring systemic acquired resistance against multiple pathogens (Misra and Saxena, 2009). In addition, JAs regulate numerous processes critical for plant development such as embryogenesis; Arabidopsis reproductive organ development; flower sex determination; seed germination; seedling growth and root development; fruit ripening; leaf movement and senescence cell expansion, growth and diploid parthenogenesis gravitropic responses tuber formation (Wasternack, 2014).

These results indicate that jasmonic acid is a potent regulator of acclimation to a broad spectrum of abiotic stresses, such as drought, salinity, high temperature, cold and heavy metal stress (Vanwallendael et al., 2019(. It is specifically responsible for the maintenance of ionic balance. A good example is the improved tolerance to alkaline stress induced by sodium carbonate (Na_2CO_3) in jasmonic acid-treated maize seedlings. This enhancement was ascribed to relieving the adverse impact of sodium carbonate on growth parameters, namely photosynthesis and total plant growth. In another study, better tolerance was associated with reduced sodium uptake and minimized oxidative damage by reducing ROS accumulation (Mir et al., 2018).

What remains unclear is the effect of increased CO_2 on salicylic acid (SA) and jasmonic acid (JA) (Zhou et al., 2019b; Kazan, 2018; Geng et al., 2016). However, it is commonly thought that high levels of CO_2 induce the biosynthesis of SA (Kazan, 2018), which in turn suppresses the synthesis of JA. In a specific example, elevated CO_2 reduces the JA content in tea leaves by inhibiting the activity or expression of lipoxygenase (LOX), an important enzyme involved in the JA synthetic pathway (Li et al., 2019).

Brassinosteroids (BRs)

Brassinosteroids (BRs), which have been identified as a class of plant hormones, were originally discovered in pollen from Brassica napus (rapeseed) because of their growth-promotion activity (Mitchell et al. 1970). The BR stimulates plant cell elongation and division, thus it should be. Now molecular characterization of BR action in a broad range of species, from green algae to flowering plants, has revealed striking diversity among chemically distinct BRs. They occur in every part of the plant — leaves stems, roots, flowers, pollen and seeds (Ohnishi 2018). BRs are steroidal hormones essential for many aspects of plant development and growth such as cell division, cell expansion; reproduction and adaptation to low-light conditions. Although it is present in different plant organs, seeds, pollens and fruits have been shown to contain significantly more of it compared to other plant parts (Li and He, 2020). Wu et al. Similarly, (2019) showed that the biosynthetic genes of both early and late pathways in BRs were upregulated by elevated CO_2 concentrations, which is assumed to contribute to stimulating BR accumulation in Pinus massoniana (Masson pine).

Conclusion

Elevated CO_2 levels significantly influence hormonal systems, enhancing growth while complicating stress responses. These effects highlight the importance of adopting adaptive agricultural strategies, such as improved crop varieties and optimized water management, to ensure sustainable productivity under changing climatic conditions. Understanding these dynamics is crucial for optimizing agricultural practices under climate change. Further research should focus on elucidating molecular mechanisms to mitigate CO_2-induced hormonal imbalances and improve crop resilience.

REFERENCES

Ahammed, G. J., Guang, Y., Yang, Y., & Chen, J. (2021). Mechanisms of elevated CO2-induced thermotolerance in plants: The role of phytohormones. Plant Cell Reports, 40(12), 2273-2286. https://link.springer.com/article/10.1007/s00299-021-02751-z

Ahammed, G. J., Li, X., Liu, A., & Chen, S. (2020). Physiological and defense responses of tea plants to elevated CO2: A review. Frontiers in Plant Science. https://doi.org/10.3389/fpls.2020.00305 .

Ali, J., Mukarram, M., Ojo, J., Dawam, N., Riyazuddin, R., Ghramh, H. A., Khan, K. A., Chen, R., Kurjak, D., & Bayram, A. (2024). Harnessing phytohormones: Advancing plant growth and defence strategies for sustainable agriculture. Physiologia Plantarum, 176(3), Article e14307.

Al-jumaili, M. A. M., & abood ALmohammedi, A. N. (2023). Effect of Spraying with Different Concentrations of Arginine and Tryptophan on the Growth and Yield of Genotypes of Hibiscus sabdarriffa L. Journal of Medical and Industrial Plant Sciences, 1.(1)

Awan, F. K., Khurshid, M. Y., & Mehmood, A. J. (2017). Plant growth regulators and their role in abiotic stress management. International Journal of Innovative Research in Biosciences, 1, 9-21.

Bharath, P., Gahir, S., & Raghavendra, A. S. (2021). Abscisic acid-induced stomatal closure: An important component of plant defense against abiotic and biotic stress. Frontiers in Plant Science, 12, Article 615114. https://doi.org/10.3389/fpls.2021.615114

Boonman, A., Prinsen, E., Gilmer, F., Schurr, U., Peeters, A., Voesenek, L., & Pons, T. L. (2007). Cytokinin import rate as a signal for photosynthetic acclimation to canopy light gradients. Plant Physiology, 143(4), 1841-1852. https://doi.org/10.1104/pp.106.094631

Chater, C., Peng, K., Movahedi, M., Dunn, J. A., Walker, H. J., Liang, Y.-K., & Wilson, I. (2015). Elevated CO2-induced responses in stomata require ABA and ABA signaling. Current Biology, 25, 2709-2716.

Cheong, J. J., and Choi, Y. D. (2003). Methyl jasmonate as a vital substance. Trends Genet. 19, 409–413. doi: 10.1016/S0168-9525(03)00138-0.

Cornforth, J. W., Milborow, B. V., Ryback, G., & Wareing, P. F. (1965). Identity of sycamore 'dormin' with abscisin II. Nature, 205, 1269-1270. https://doi.org/10.1038/2051269b0

D'Agostino, I. B., & Kieber, J. J. (1999). Molecular mechanisms of cytokinin action. Current Opinion in Plant Biology, 2, 359-364.

Daviere, J. M., & Achard, P. (2015). A pivotal role of DELLAs in regulating multiple hormone signals. Molecular Plant. https://doi.org/10.1016/j.molp.2015.09.011

Dobránszki, J., & Drienyovszki, N. M. (2014). Cytokinin-induced changes in the chlorophyll content and fluorescence of in vitro apple leaves. Journal of Plant Physiology, 171(16), 1472-1478. https://doi.org/10.1016/j.jplph.2014.06.015

Droulia, F., & Charalampopoulos, I. (2021). Future climate change impacts on European viticulture: A review on recent scientific advances. Atmosphere, 12, Article 495. https://doi.org/10.3390/atmos12040495

Fan, N., Yang, Z., Hao, T., Zhuang, L., Xu, Q., & Yu, J. (2022). Differential effects of elevated atmosphere CO2 concentration on root growth in association with regulation of auxin and cytokinins under different nitrate supply. Environmental and Experimental Botany, 201, Article 104943. https://doi.org/10.1016/j.envexpbot.2022.104943

Fang, L., Abdelhakim, L. O. A., Hegelund, J. N., Li, S., Liu, J., Peng, X., Li, X., Wei, Z., & Liu, F. (2019). ABA-mediated regulation of leaf and root hydraulic conductance in tomato grown at elevated CO2 is associated with altered gene expression of aquaporins. Horticultural Research, 6, Article 104. https://doi.org/10.1038/s41438-019-0187-6

Finkelstein, R. (2013). Abscisic acid synthesis and response. The Arabidopsis book/American society of plant biologists, 11.

Finlayson, S. A., & Reid, D. M. (1996). The effect of CO2 on ethylene evolution and elongation rate in roots of sunflower (Helianthus annuus) seedlings. Physiologia Plantarum, 98, 875-881.

Gamage, D., Thompson, M., Sutherland, M., Hirotsu, N., Makino, A., & Seneweera, S. (2018). New insights into the cellular mechanisms of plant growth at elevated atmospheric carbon dioxide concentrations. Plant, Cell & Environment, 41(6), 1233-1246. https://doi.org/10.1111/pce.13206

Gan, L., Song, M., Wang, X., Yang, N., Li, H., Liu, X., & Li, Y. (2022). Cytokinins is involved in regulation of tomato pericarp thickness and fruit size. Horticultural Research, 19, Article 4.

Gangappa, S. N., & Botto, J. F. (2016). The multifaceted roles of HY5 in plant growth and development. Molecular Plant, 9(10), 1353-1365. https://doi.org/10.1016/j.molp.2016.07.002

Gasparini, K., Costa, L. C., Brito, F. A. L., Pimenta, T. M., Cardoso, F. B., Araújo, W. L., Zsögön, A., & Ribeiro, D. M. (2019). Elevated CO2 induces age-dependent restoration of growth and metabolism in gibberellin-deficient plants. Planta, 250(4), 1147-1161. https://doi.org/10.1007/s00425-019-03208-0

Geiss, G., Gutierrez, L., & Bellini, C. (2018). Adventitious root formation: New insights and perspectives. In Annual plant reviews online (pp. 127-156). https://doi.org/10.1002/9781119312994.apr0400

Geng, S., Misra, B. B., de Armas, E., Huhman, D. V., Alborn, H. T., Sumner, L. W., & Chen, S. (2016). Jasmonate-mediated stomatal closure under elevated CO2 revealed by time-resolved metabolomics. The Plant Journal, 88(6), 947-962. https://doi.org/10.1111/tpj.13296

Gupta, P., Duplessis, S., White, H., Karnosky, D., Martin, F., & Podila, G. (2005). Gene expression patterns of trembling aspen trees following long-term exposure to interacting elevated CO2 and tropospheric O3. New Phytologist, 167, 129-142.

Guschina, I. A., Harwood, J. L., Smith, M., & Beckett, R. P. (2002). Abscisic acid modifies the changes in lipid brought about by water stress in the moss (Atrichum androgynum). New Phytologist, 156, 255-264. https://doi.org/10.1046/j.1469-8137.2002.00517.x

Gutiérrez-Mañero, F. J., Ramos-Solano, B., Probanza, A. N., Mehouachi, J. R., Tadeo, F., & Talon, M. (2001). The plant-growth promoting rhizobacteria Bacillus pumilus and Bacillus licheniformis produce high amounts of physiologically active gibberellins. Physiologia Plantarum, 111(2), 206-211.

Hassan, S. B. (2023). Impact of humic acid and benzyl adenine Spraying on Coriander Plant Development and yield (Coriandrum sativum L.). Journal of Medical and Industrial Plant Sciences.

Hayat, S., & Ahmad, A. (2007). Salicylic Acid: A Plant Hormone. Springer. https://doi.org/10.1007/1-4020-5184-0

He, M., He, C.-Q., and Ding, N.-Z. (2018). Abiotic stresses: general defenses of land plants and chances for engineering multistress tolerance. Front. Plant Sci. 9, 1771. doi: 10.3389/fpls.2018.01771.

Hedden, P., & Phillips, A. L. (2000). Gibberellin metabolism: New insights revealed by the genes. Trends in Plant Science, 5(12), 523-530. https://doi.org/10.1016/s1360-1385(00)01790-8

Hönig, M., Plíhalová, L., Husičková, A., Nisler, J., & Doležal, K. (2018). Role of cytokinins in senescence, antioxidant defense and photosynthesis. International Journal of Molecular Sciences, 19(12), Article 4045. https://doi.org/10.3390/ijms19124045

Horváth, E., Pál, M., Szalai, G., Páldi, E., and Janda, T. (2007). Exogenous 4-hydroxybenzoic acid and salicylic acid modulate the effect of short-term drought and freezing stress on wheat plants. Biol. Plantarum 51, 480–487. doi: 10.1007/s10535-007-0101-1.

Iqbal, M. A. (2015). Role of moringa, brassica and sorghum water extracts in increasing crops growth and yield: A review. American-Eurasian Journal of Agricultural and Environmental Sciences, 14, 1150-1158. https://doi.org/10.5829/idosi.aejaes.2014.14.11.12436

Jordi, W., Schapendonk, A., Davelaar, E., Stoopen, G. M., Pot, C. S., de Visser, R., van Rhijn, J. A., Gan, S., & Amasino, R. M. (2000). Increased cytokinin levels in transgenic P(SAG12)-IPT tobacco plants have large direct and indirect effects on leaf senescence, photosynthesis and N partitioning. Plant, Cell & Environment, 23(3), 279-289. https://doi.org/10.1046/j.1365-3040.2000.00544.x

Jurado, S., Abraham, Z., Manzano, C., López-Torrejón, G., Pacios, L. F., & Del Pozo, J. C. (2010). The Arabidopsis cell cycle F-box protein SKP2A binds to auxin. The Plant Cell, 22, 3891-3904. https://doi.org/10.1105/tpc.110.078972

Kazan, K. (2018). Plant-biotic interactions under elevated CO2: A molecular perspective. Environmental and Experimental Botany, 153, 249-261. https://doi.org/10.1016/ j.envexpbot.2018.06.005

Kendrick, M. D., & Chang, C. (2008). Ethylene signaling: New levels of complexity and regulation. Current Opinion in Plant Biology, 11, 479-485. https://doi.org/10.1016/ j.pbi.2008.06.011

Kosakivska, I. V., Vedenicheva, N. P., Babenko, L. M., Voytenko, L. V., Romanenko, K. O., & Vasyuk, V. A. (2022). Exogenous phytohormones in the regulation of growth and development of cereals under abiotic stresses. Molecular Biology Reports, 49(1), 617-628.

Kovtun, Y. W., Chiu, W. L., Tena, G., & Sheen, J. (2000). Functional analysis of oxidative stress-activated mitogen-activated protein kinase cascade in plants. Proceedings of the National Academy of Sciences, 97, 2940-2945. https://doi.org/10.1073/pnas.97.6.2940

Lee, S. B., & Suh, M. C. (2015). Advances in the understanding of cuticular waxes in Arabidopsis thaliana and crop species. Plant Cell Reports, 34, 557-572. https://doi.org/10.1007/s00299-015-1772-2

Li, X., Kristiansen, K., Rosenqvist, E., & Liu, F. (2019). Elevated CO2 modulates the effects of drought and heat stress on plant water relations and grain yield in wheat. Journal of Agronomy and Crop Science, 205(4), 362-371. https://doi.org/10.1111/jac.12330

Li, Z., & Ahammed, G. J. (2023). Salicylic acid and jasmonic acid in elevated CO2-induced plant defense response to pathogens. Journal of Plant Physiology, 286, Article 154019.

Li, Z., & He, Y. (2020). Roles of brassinosteroids in plant reproduction. International Journal of Molecular Sciences, 21(3), Article 872. https://doi.org/10.3390/ijms21030872

Mir, M. A., John, R., Alyemeni, M. N., Alam, P., & Ahmad, P. (2018). Jasmonic acid ameliorates alkaline stress by improving growth performance, ascorbate glutathione cycle and glyoxylase system in maize seedlings. Scientific Reports, 8, Article 2831. https://doi.org/10.1038/s41598-018-21097-3

Mishra, A. K., & Baek, K. H. (2021). Salicylic acid biosynthesis and metabolism: A divergent pathway for plants and bacteria. Biomolecules, 11(5), Article 705. https://doi.org/10.3390/ biom11050705

Misra, N., & Saxena, P. (2009). Effect of salicylic acid on proline metabolism in lentil grown under salinity stress. Plant Science, 177(3), 181-189.

Mitchell, J., Mandava, N., Worley, J., Plimmer, J., & Smith, M. (1970). Brassins—A new family of plant hormones from rape pollen. Nature, 225, 1065-1066. https://doi.org/10.1038/2251065a0

Noman, Ali, A., Aqeel, M., Qari, S. H., Al Surhanee, A. A., Yasin, G., Alamri, S., Hashem, M., & Al-Saadi, A. M. (2020). Plant hypersensitive response vs pathogen ingression: Death of few gives life to others. Microbial Pathogenesis, 145, Article 104224. https://doi.org/10.1016/j.micpath.2020.104224

Ohnishi, T. (2018). Recent advances in brassinosteroid biosynthetic pathway: Insight into novel brassinosteroid shortcut pathway. Journal of Pesticide Science, 43, 159-167. https://doi.org/10.1584/jpestics.D18-040

Plackett, A. R. G., & Wilson, Z. A. (2016). Gibberellins and plant reproduction. In Annual plant reviews: The gibberellins (Vol. 49, pp. 323-358). John Wiley & Sons. https://doi.org/10.1002/9781119210436.ch11

Potters, G., Pasternak, T. P., Guisez, Y., & Jansen, M. A. (2009). Different stresses, similar morphogenic responses: Integrating a plethora of pathways. Plant, Cell & Environment, 32, 158-169. https://doi.org/10.1111/j.1365-3040.2008.01908.x

Ribeiro, D. M., Mueller-Roeber, B., & Schippers, J. H. M. (2013). Promotion of growth by elevated carbon dioxide is coordinated through a flexible transcriptional network in Arabidopsis. Plant Signaling & Behavior, 8(3). https://doi.org/10.4161/psb.23356

Sabagh, E. A., Islam, M. S., Hossain, et al., (2022). Phytohormones as growth regulators during abiotic stress tolerance in plants. Frontiers in Agronomy, 4, Article 765068. https://doi.org/10.3389/fagro.765068

Sairanen, I., Novák, O., Pěnčík, A., Ikeda, Y., Jones, B., Sandberg, G., Ljung, K., & Kakimoto, T. (2012). Soluble carbohydrates regulate auxin biosynthesis via PIF proteins in Arabidopsis. The Plant Cell, 24, 4907-4916. https://doi.org/10.1105/tpc.112.104794

Sapna, Mishra, Roychowdhury, R., Ray, S., Hada, A., Kumar, A., Sarker, U., Aftab, T., & Das, R. (2024). Salicylic acid (SA)-mediated plant immunity against biotic stresses: An insight on molecular components and signaling mechanism. Plant Stress, 11, Article 100427. https://doi.org/10.1016/j.stress.2024.100427

Seneweera, S., Aben, S., Basra, A., Jones, B., & Conroy, J. (2003). Involvement of ethylene in the morphological and developmental response of rice to elevated atmospheric CO2 concentrations. Plant Growth Regulation, 39, 143-153.

Shi, Y., Tian, S., Hou, L., Huang, X., Zhang, X., Guo, H., et al. (2012). Ethylene signaling negatively regulates freezing tolerance by repressing expression of CBF and type-A ARR genes in Arabidopsis. Plant Cell 24, 2578–2595. doi: 10.1105/tpc.112.098640.

Singhal, R. K., Saha, D., Skalicky, M., Mishra, U. N., Chauhan, J., Behera, L. P., Chand, J., & Varshney, S. K. (2021). Crucial cell signaling compounds crosstalk and integrative multi-omics techniques for salinity stress tolerance in plants. Frontiers in Plant Science, 12, Article 670369. https://doi.org/10.3389/fpls.2021.670369

Sosnowski, J., Truba, M., & Vasileva, V. (2023). The impact of auxin and cytokinin on the growth and development of selected crops. Agriculture, 13(3), Article 724. https://doi.org/10.3390/agriculture13030724

Teng, N., Wang, J., Chen, T., Wu, X., Wang, Y., & Lin, J. (2006). Elevated CO2 induces physiological, biochemical and structural changes in leaves of Arabidopsis thaliana. New Phytologist, 172, 92-103.

Tromas, A., Braun, N., Muller, P., Khodus, T., Paponov, I. A., Palme, K., Ljung, K., Lee, J.-Y., Benfey, P., Murray, J. A. H., Scheres, B., & Perrot-Rehomann, C. (2009). The auxin binding protein 1 is required for differential auxin responses mediating root growth. PLoS ONE, 4(9), Article e6648. https://doi.org/10.1371/journal.pone.0006648

Urbanova, T., & Leubner-Metzger, G. (2016). Gibberellins and seed germination. Annual Plant Reviews, 49, 253-284.

Vanwallendael, A., Soltani, A., Emery, N. C., Peixoto, M. M., Olsen, J., & Lowry, D. B. (2019). A molecular view of plant local adaptation: Incorporating stress-response networks. Annual Review of Plant Biology, 70, 559-583. https://doi.org/10.1146/annurev-arplant-050718-100114

Wasternack, C. (2014). Action of jasmonates in plant stress responses and development—applied aspects. Biotechnology advances, 32(1), 31-39.

Wei, H., Gou, J., Yordanov, Y., Zhang, H., Thakur, R., Jones, W., & Burton, A. (2013). Global transcriptomic profiling of aspen trees under elevated [CO 2] to identify potential molecular mechanisms responsible for enhanced radial growth. Journal of plant research, 126, 305-320.

Wu, C., Li, F., Xu, H., Zeng, W., Yu, R., Wu, X., ... & Li, J. (2019). The potential role of brassinosteroids (BRs) in alleviating antimony (Sb) stress in Arabidopsis thaliana. Plant Physiology and Biochemistry, 141, 51-59.

Yang, C., Li, W., Cao, J., Meng, F., Yu, Y., Huang, J., et al. (2017). Activation of ethylene signaling pathways enhances disease resistance by regulating ROS and phytoalexin production in rice. Plant J. 89, 338–3531. doi: 10.1111/tpj.13388.

Yin, Y., Jiang, X., Ren, M., Xue, M., Nan, D., Wang, Z., ... & Wang, M. (2018). AmDREB2C, from Ammopiptanthus mongolicus, enhances abiotic stress tolerance and regulates fatty acid composition in transgenic Arabidopsis. Plant Physiology and Biochemistry, 130, 517-528.

Zhang, H., Pan, C., Gu, S., Ma, Q., Zhang, Y., Li, X., & Shi, K. (2019). Stomatal movements are involved in elevated CO2-mitigated high-temperature stress in tomato. Physiologia plantarum, 165(3), 569-583.

Zhang, S., Li, X., Sun, Z., Shao, S., Hu, L., Ye, M., ... & Shi, K. (2015). Antagonism between phytohormone signaling underlies the variation in disease susceptibility of tomato plants under elevated CO2. Journal of Experimental Botany, 66(7), 1951-1963.

Zhou, Y., Ge, S., Jin, L., Yao, K., Wang, Y., Wu, X., ... & Yu, J. (2019b). A novel CO 2-responsive systemic signaling pathway controlling plant mycorrhizal symbiosis. New Phytologist, 224(1), 106-116.

Zhou, Y., Van Leeuwen, S. K., Pieterse, C. M., Bakker, P. A., & Van Wees, S. C. (2019a). Effect of atmospheric CO2 on plant defense against leaf and root pathogens of Arabidopsis. European Journal of Plant Pathology, 154, 31-42.

Zinta, G., Abd-Elgawad, H., Peshev, D., Weedon, J. T., Van den Ende, W., Nijs, I.. & Asard, H. (2018). Dynamics of metabolic responses to periods of combined heat and drought in Arabidopsis thaliana under ambient and elevated atmospheric CO2. Journal of Experimental Botany, 69(8), 2159-2170.