Biostimulants Boost Date Palm's Performance under Abiotic Stresses

Subjects: Plant Sciences

Contributor: Fatima-Zahra Akensous , Mohamed Anli , Abdelilah Meddich

Date palm (*Phoenix dactylifera* L.) is constantly hindered due to detrimental abiotic constraints. Thus, there is a crucial need to deal with this problem. The application of biostimulants, such as the arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), and organic amendments hold tremendous potential to ameliorate the growth and yield of date palm significantly. The strengthening of biostimulants' main common modes of action is exerted through five main functions: biostimulation (essentially), biofertilization, bioprotection, biological control, and the role of bio-effector. Moreover, synergistic and complementary effects manifest through biochemical and nutritional benefits, as well as molecular modulation. In this sense, available data provide suggestive findings that corroborate the beneficial roles of biostimulants, thereby positioning them as promising eco-friendly tools that work toward resilience to abiotic stresses in date palm.

biostimulants date palm drought heavy metal(oid)s resilience salinity

1. Introduction

Climate models indicate a projected intensification of climate change events, marked by alterations in frequency and severity. In addition, global warming is indicated to have serious consequences on the biosphere [1][2]. As far as the agricultural sector is concerned, consequences extend to affecting food security and livelihoods worldwide [3]. Thus, it is important to produce high-yielding and resilient crops [4]. On the other hand, the ever-growing global population is anticipated to reach almost 10 billion by 2050, 5 of which are threatened by living in regions with absolute water shortages. Moreover, food requirements for agriculture are predicted to double by 2050 [5]. There exists a range of environmental constraints, also known as abiotic stresses that negatively affect plants' performance. Among these abiotic constraints, drought, salinity, and heavy metal(oid) stresses stand out as the most serious ones [6][7]. Globally, the agricultural sector accounts for about 70% of freshwater withdrawals [8]. On the other hand, 7% of the total land area is negatively impacted by soil salinity [9]. The major hurdles imposed by salinity are mainly ionic and osmotic tensions that lead to a major disturbance in ion equilibrium and cause sodium chloride toxicity. Consequently, the functioning of several enzymes, as well as cell metabolism, end up being negatively impacted [10]. Poorer irrigation has been leading to soil poisoning due to excess salt. Thus, salt tends to accumulate on soil surfaces via capillary movement, which leads to the soil's degradation and yield decline [11]. Heavy metal(oid)s represent major threats to the environment, notably soils and plants. Generally, plants grown under heavy metal(oid)s contamination tend to accumulate excessive amounts of these elements. As a major consequence, plants' growth performance and productivity become severely hindered, in addition to the deterioration of the contaminated soils [12]. Therefore, it is crucial to determine how plants deal with abiotic stresses on a molecular basis [13].

Date palm represents the oases' most relevant crop. Its most important product, the dates, is a highly nutritious fruit with multiple healthy benefits [14][15]. Date palm can partly withstand extreme environmental conditions, thanks to its plasticity properties. However, date palm remains severely endangered by abiotic stresses; for instance, drought stress affects the leaf size, extension of stems, proliferation of roots, and water–plant relations [16][17][18]. On this account, plants such as date palm have learned to acquire the capacity of modulating the vegetative and reproductive stages in function of the surrounding abiotic stresses. A set of adaptive mechanisms occur within date palm, particularly the expression regulation of a wide array of abiotic-stress-related genes. On the biochemical level, the restricted assimilation of CO_2 by leaves, due to stomatal *closure*, leads to the enhancement of the photorespiratory pathway, bringing about oxidative damage and the overproduction of reactive oxygen species (ROS). Hence, plants adapt by reducing transpirational losses and switching to smaller leaves, thereby reducing the surface area and enhancing the leaf thickness [19]. Moreover, plants overaccumulate osmolytes, such as total soluble sugars and proteins, proline, and glycine betaine, which contributes to maintaining vital cellular functions [20]. In addition, plants produce key enzymatic and nonenzymatic antioxidant molecules that play a key role in detoxifying ROS. In this regard, plant hormones exert a major role in the regulation of abiotic stressors [21]. In addition to genes, varied transcription factors (TFs), such as the dehydration-responsive element-binding (DREB) gene, aquaporins (AQPs), late embryogenesis abundant proteins (LEA), and dehydrins, have been shown to enhance plants' resilience to environmental stressors [22]. In this regard, computer-based performances and trials, known as in silico, are helping establish the understanding on a broader level in science [23][24]. Concerning date palm, in silico technologies can assist with the identification of drought-related genes' orthologs, as well as paralogs, through genome sequencing assembly (e.g., GCA_000413155.1) [25], sequence assessment of salt-related stress proteins relying on bioinformatics databases (e.g., National-Center of Biotechnology Information, goes also by the acronym NCBI) [26], and quantitative PCR to detect genes' expression in relation with heavy metal(oid)s [27], for example. Hence, in silico investigation can provide insightful results regarding the molecular pathways undergone by date palm plants to withstand different abiotic stresses [28].

Biostimulants are a set of organic materials and/or microorganisms that can enhance water assimilation, nutrient uptake, and resilience to abiotic stresses. They represent an innovative and eco-friendly option for sustainable agriculture goals, thanks to a plethora of benefits [29]. Among biostimulants, the arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), as well as organic amendments (compost and manure) work out as the most implicated in agriculture, thanks to a plethora of beneficial roles in both plants and soils [30][31]. AMF are soil-obligate root biotrophs that develop within around 80% of terrestrial plants. These soil beneficial microorganisms depend on plants' photosynthetic products. In exchange, they can make water and nutrients accessible to plants, especially under abiotic stresses [32]. AMF are grouped under the phylum of Glomeromycota. The phylum comprises Archaeosporomycetes, Glomeromycetes, and Paraglomeromycetes classes; Archaeosporales, Diversisporales, Gigasporales, Glomerales, and Paraglomerales orders; in addition to 14 families, 29 genera, and over 240 species. Some of the most studied AMF species are *Funneliformis mosseae*, *Gigaspora* spp., and *Rhizophagus irregularis* [33]. PGPR are a group of rhizospheric bacteria that associate with the root system of plants. They can ameliorate the growth performance and yield of plants by producing indole-3-acetic acid (IAA), ammonia (NH_3), and hydrogen cyanide (HCN), among other components. In addition, PGPR regroup diverse genera, such as *Pseudomonas*, *Klebsiella*, and *Bacillus*. Different roles can be played by PGPR; they can fix nitrogen (N), solubilize phosphorus (P), decrease heavy metal(oid)s pollution, produce plant hormones, mineralize the organic matter in soils, and provide resilience to abiotic stresses [34][35]. Furthermore, compost constitutes the final product of organic material decomposition [36]. Compost assures several beneficial effects; it essentially serves as a growth medium, an organic fertilizer, a soil amendment, and a water-retaining ameliorator [37]. Finally, manure is the final product of organic material decomposition, which has mostly animal origins (livestock). Manure, however, comprises organically complex nutritive plant nutrients. Its application benefits crop productivity and soil fertility [38].

Probably, biostimulants act through in-common and complementary mechanisms, which make them exert diverse functions. Therefore, biostimulants represent promising means with the potential ability to boost date palm plants' resilience to abiotic stresses.

2. History and Distribution of Date Palm

Probably, date palm might be the oldest plant in the world [39], as well as the most relevant crop of the fertile ecosystems situated in the oases. Date palm's origin and distribution remain debatable; while remote locations of Oman are believed to be the cradle of this iconic crop, domestication history remains uncertain. Chances are the domestication of date palm plants occurred in the Mesopotamia–Arabic Gulf area from the late 4th or early 3rd millennium before the common era (BCE), then spread later over Africa. A generated online database intended to assess date palm plants' genomic resources, with precise locations of polymorphic microsatellite loci in 62 cultivars, could supply valuable information [40]. On the other hand, 1963–1965 excavations of a Herodian fortress that dates back to the 1st century BCE revealed the presence of ancient date palm seeds that could germinate. A comparison of three elite cultivars by the means of random amplified polymorphic DNA disclosed that 50% of generated DNA bands showed similarities to Moroccan "Medjool", Egyptian "Hayani", and Iraqi "Barhee" cultivars. In addition, fewer differences in polymorphic bands were noted between ancient seeds and the Iraqi cultivar [41].

Historically, the cultivation of date palm plants is believed to have started in the Northern African and Middle Eastern areas. This is linked to pollen grains that date back to 50,000–33,000 years before the present (YBP), which were found in the Northern part of Iraq, and charcoal observed in Ohalo II from Northern Israel dating back to 19,000 YBP. Later on, date palm found its way to popularization within new spots in the world, such as Australia, South Asia, Southern Africa, and the Americas, during the preceding three centuries [39].

3. Date Palm, A Pillar in the Oasis Ecosystem

Date palm grows mainly in the drastic arid parts of the Northern African and Middle Eastern areas. It belongs to the genus *Phoenix*, which makes for 14 perennial monocotyledonous species of the Arecaceae family [39][40]. Date palm holds an important socio-economic value amongst leading countries growing the crop for its most appreciated fruits: the dates [42][43]. Dates comprise more than 60% of carbohydrates, 10% of lipids, and 5% of proteins. In addition, they represent a major source of sterols, estrone, soluble polysaccharides, and tannins [44]. Date palm plays a key role in ameliorating food security in rural and dry regions, as well as sustaining ecological balance and stabilizing the soil. Moreover, it helps fight soil desertification and erosion [45].

4. Pests, Diseases, and Anthropogenic Constraints

Date palm is continuously subjected to biotic stresses, with insects and fungi being the main causal agents [45][46]. *Rhynchophorus ferrugineus*, also known as the red palm weevil, constitutes the most damaging pest infestation to date palm plants in the Middle East and Europe [47], and it has spread to North Africa as well. *Potosia opaca* is a pest that attacks the crown of *Phoenix dactylifera*, mainly the leaves' base and weakened rachis, where the larvae deposit their eggs. Thus, this insect beetle contributes to the deterioration of date palm groves, especially in North Africa where it was first observed (*Potosia opaca* var. cardui Gyllenhal). Moreover, North Africa is dealing with a fungal disease that goes by the name of Bayoud (*Fusarium oxysporum* f. sp. *albedinis*), having already finished off some 13 million date palm plants of Morocco and Algeria, intensifying desertification [48]. Additionally, date palm plants are often infested with *Ceratocystis paradoxa* and *C. radicicola*, two fungal species that can distress about any part of the plant [49].

Date palm populations are influenced by anthropogenic actions, mainly due to overgrazing and low maintenance, which leads to the loss of vegetation cover and increasing the intensity of extreme climatological events, such as windy velocity that results in both reduced levels of the water table and infiltration to the soils [39][42].

5. Effects of Abiotic Stresses and Adaptive Strategies in Date Palm

Drought stress, salinity, and heavy metal(oid)s pollution count as aggressive environmental factors to plants such as *P. dactyliphera*. The detrimental effects of abiotic stressors go beyond merely date palm's growth since they extend to yield and productivity, as presented in **Table 1**. However, date palm plants learned to adapt to the environing constraints, thanks to a plethora of mechanisms. Plants' adaptation to drastic environmental constraints depends on the genomic evolution potential and acclimatization proceedings. Plants act by two main strategies in response to abiotic stresses: stress avoidance and stress resilience. Plants opt for stress avoidance through alternatives such as growth decrease, early flower blooming, senescence acceleration, and yield reduction. On the other hand, developing resilience to abiotic stresses relies upon maintaining the plants' cellular, molecular, and metabolic functioning [50].

Table 1. Impact of drought, salinity, and heavy metal(oid) stresses on date palm.

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
Drought	Watering cessation for 7–8 days before harvest	Seedlings	-	Heat-shock proteins (HSPs), chaperone proteins, and heat stress Transcription Factors (TFs) genes' expression Cell death elimination Enrichment of phytohormones-related, wax, secondary metabolism, fatty acids biosynthesis, and plant cell wall pathways	[17]
Drought	70%, 100% evapotranspiration (ETc)	10–12-year-old orchards	"Mazafati"	Increase in bunch weight, fruit weight, fruit starch, yielding, and water-use efficiency (WUE) Increase in soluble solids and sugar content	[51]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
				A rise in total phenolic compounds, peroxidase (POX), polyphenol Amelioration of (PPO) activities A rise in calcium (Ca), iron (Fe), and zinc (Zn)	
Drought	6.9, 13.95, 27.5% of polyethylene glycol 6000 (PEG)	3 month seedlings	“Sagie”	Enhancement of phenolic and flavonoid content Rise of Catalase (CAT), peroxidase (POX), and polyphenol oxidase (PPO) activities	[52]
Drought	0 (control), −0.41, −0.82, −1.23, −1.63 MPa of mannitol	4–5-year-old suckers	“Barhee”, “Ruziz”, “Sukary”	Decrease in leaf and root numbers, leaf, and root dry weights,	[53]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
				and total dry weight A decline in relative water content (RWC), photosynthetic and rate of transpiration, water-use efficiency (WUE), and mesophyll conductance Increase in $[CO_2]_i$	
Drought	Irrigation reduced to 50% of the control	2 year old seedlings	-	Decrease in shoot growth A decline in leaf gas exchange Decrease in intrinsic leaf water-use efficiency (WUEi)	[54]
Drought	Gradual decline in humidity	Plantlets	“Sewi”	Dehydration A decline in photosynthetic pigments Decline in surviving chances	[55]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
Drought	Irrigation reduced to 50% of the control	2-year-old seedlings	-	Decrease in leaf hydration, foliar total and reduced ascorbate, chlorophyll a/b ratio, sugars, and organic acids Increase in total reduced glutathione (GSH), oxidized glutathione (GSSG), the GSSG/GSH ratio, amino acids, and 5,8,11,14-eicosatetraenoic acid	[56]
Drought	Irrigation reduced to 50% and 25% of the control	2-year-old plants	-	A rise in isoprene emission rates and a decline in soil water content (SWC) Upregulation of primary metabolism, stress	[25]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
				response, photosynthesis, and antioxidant-related proteins Downregulation of gene expression, metabolic, and secondary metabolism-related proteins	
Drought	50, 100, 150% of evapotranspiration levels	*Trees*	"Succary"	A decline in date palm yielding Affected fruit traits An overall decline in fruit metabolites	[57]
Drought	50, 75, 100% of watering demand	*Trees*	"Khalas"	Affected fruit yielding as well as quality	[58]
Salinity	0, 240 mM NaCl	Seedlings	"Khalas", "Manoma", "Barni", "Nashukharma", "Hilali-Omani", "Fard", "Abunarenja", "Nagal", "Umsila", "Zabad"	Reduction in shoot as well as root dry weights, and leaf area Decrease	[59]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
				in photosynthetic properties	
Salinity	50, 100, 150 mM NaCl	2 month seedlings	“Khalas”	Enhancement of proline content and thiobarbituric acid reactive substances (TBARS) A rise in Catalase (CAT) as well as Superoxide Dismutase (SOD) activities Variation within cDNA start codon-targeted (cDNASCoT) marker genes’ expression	[60]
Salinity	5, 10, 15 dS m^{-1} of salt water	*Trees*	“Ajwat AlMadinah”, “Naghal”, “Khnizi”, “Barhi”, “Makhtoumi”, “Farad”, “Khisab”, “Nabtat-Saif“, “Shagri”,	Excluding of Na^+ Retaining of K^+ Decrease in osmotic potential	[61]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
			"Abu-Maan", "Jabri", "Sukkari", "Rothan"		
Salinity	0, 300 mM NaCl	Seedlings	"Khalas"	Decline in photosynthetic capacity, stomatal conductance (gs), rate of transpiration (E), as well as internal carbon dioxide concentration $[CO_2]_i$ Variation within genes expression Transcripts enrichment implicated in metabolism pathways	[62]
Salinity	50, 300 mM NaCl	Seedlings	"Khalas"	Decrease in photosynthetic capacity, stomatal conductance (gs),	[63]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
				rate of transpiration (E), and root system traits Hypermethylated and hypomethylated DNA regions, coupled with insignificant genes expression	
Salinity	0, 240 mM NaCl	Seedlings	"Umsila", "Zabad"	Decrease in leaf area, physiological traits, and leaf water potential (LWP) Increase in leaf total soluble sugars, proline and glycine betaine	[64]
Salinity	0, 240 mM NaCl	Seedlings	"Umsila", "Zabad"	A decline in leaf fresh and dry weights	[65]
Salinity	0, 300 mM NaCl	Seedlings	"Khalas"	Decrease in leaf area, leaf and root dry weights, K^+	[66]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
				accumulation, and roots' Casparian strips Enhancement of stress-related metabolites (e.g., osmolytes and antioxidant enzymes)	
Salinity	5 dS m^{-1}, 15 dS m^{-1} of saline water	*Trees*	"Lulu", "Khalas", "Shahlah"	Negative effect on height Decrease in tree water use (ETc) Variation in the consumed water productivity (CWP)	[67]
Salinity	<1, 12–15, 18–20 dS m^{-1} of saline	4-year-old *trees*	-	A decline in actual water use	[68]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
	water				
Salinity	5, 10, 15 dS m^{-1} of salt water	*Trees*	-	Decrease in trunk height and diameter, brunch total number, yielding of dates Increase in canopy temperature (CT)	[69]
Salinity	4 g/L, 8 g/L, 12 g/L, 16 g/L NaCl	Seedlings	"Deglet Nour"	Drop in seeds' germination, radicle length, and Catalase (CAT) activity A rise in total protein content, superoxide dismutase (SOD), and secondary metabolites	[60]
Salinity	5, 10, 15 dS m^{-1} of salt	*Trees*	"Ajwat Al Madinah", "Naghal", "Barhi", "Shagri", "Abu Maan", "Jabri",	Increase in minerals, mainly K, P, and Ca	[70]

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
	water		“Sukkari”, “Rothan”, “Khinizi”, “Maktoumi”		
Salinity	Irrigation levels based on crop evapotranspiration (ETc) at 50%, 100%, and 150% of saline water	*Trees*	“Succary”	Decrease in dates yielding, fruit weight and size, total soluble solids (TTS), acidity, fruit moisture content, and total sugar and non-reducing sugar content in fruits	[57]
Salinity	0, 240 mM NaCl	Seedlings	“Umsila”, “Zabad”	Production of salinity-related metabolites	[71]
Salinity	3.2–4.5 dS m^{-1} salt water (ECw)	*Trees*	-	Increase in transpiration, soil evaporation, percolation, and salt accumulation	[72]

11. Shahid, S.A.; Zaman, M.; Heng, L.. Introduction to Soil Salinity, Sodicity and Diagnostics Techniques; Springer: Cham: Switzerland, 2018; pp. ISBN 9783319961897.

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
Heavy metal(oid)s	Cadmium (Cd), chromium (Cr)	Seedlings	“Deglet Nour”	Decrease in phytochelatin synthase (*pcs*) and metallothionein (*mt*) genes’ expression	[73]
Heavy metal(oid)s	Antimony (Sb), cadmium (Cd), lead (Pb), chromium (Cr), arsenic (As), aluminum (Al)	Date fruits	“Sakay Mabroum”, “Kadary”, “Safawy Al-Madina”, “Eklas Al-Hassa”, “Barny Al-Madina”, “Rashadya Al-qaseem”, “Sakay Normal”	As along with Pb surpassing the maximal allowable levels (MAL)	[74]

6. Biostimulants Attenuate Abiotic Stresses’ Effects in Date Palm

Biostimulants, such as AMF, PGPR, and compost and manure, are regarded as potential substitutes for synthetic and chemical fertilizers, which can ensure food security and enable a sustainable product, thus paving the way to new approaches aiming at improving agricultural productivity [75][76]. Available data corroborate the positive impact of biostimulants on date palm, especially in terms of resilience to abiotic stresses [77] (**Table 2**).

Table 2. Effects of AMF, PGPR, and organic amendments on date palm under drought, salinity, and heavy metal(oid) stresses.

one.0177883.

18. Benaffari,W.; Boutasknit, A.; Anli, M.; Ait-El-mokhtar, M.; Ait-Rahou, Y.; Ben-Laouane, R.; Ahmed, H.B.; Mitsui, T.; Baslam, M.; Meddich, A.; et al. The Native Arbuscular Mycorrhizal Fungi and Vermicompost-Based Organic Amendments Enhance Soil Fertility, Growth Performance, and the Drought Stress Tolerance of Quinoa. *Plants* **2022**, *11*, 393, https://doi.org/10.3390/plants11030393.

19. Hasanuzzaman, M.; Hakeem, K.R.; Nahar, K.; Alharby, H.F.. Plant Abiotic Stress Tolerance: Agronomic, Molecular and Biotechnological Approaches; Springer: Cham, Switzerland, 2019; pp. Volume 7, pp. 1–490.

20. Jogawat, A.. Osmolytes and Their Role in Abiotic Stress Tolerance in Plants; In Molecular Plant Abiotic Stress; Wiley: New York: NY, USA, 2019; pp. 91–104, ISBN 9781119463665.

21. Hasanuzzaman, M.; Bhuyan, M.H.M.B.; Zulfiqar, F.; Raza, A.; Mohsin, S.M.; Al Mahmud, J.; Fujita, M.; Fotopoulos, V.; Reactive Oxygen Species and Antioxidant Defense in Plants under Abiotic Stress: Revisiting the Crucial Role of a Universal Defense Regulator. *Antioxidants* **2020**, *9*, 681, https://doi.org/10.3390/antiox9080681.

22. Sarkar, T.; Thankappan, R.; Mishra, G.P.; Nawade, B.D.; Advances in the Development and Use of DREB for Improved Abiotic Stress Tolerance in Transgenic Crop Plants. *Physiol. Mol. Biol.*

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
Drought	75, 25% FC	*Rhizoglomus irregulare* Aoufous consortium	PGPR consortium	Grass-based compost Green waste-based compost	Enhancement of growth traits and physiological parameters Improvement of N and P content Increase in sugar and protein content Decrease in MDA and H_2O_2 Decrease in soil pH and boosting of electrical conductivity (EC), organic matter (OM), and total organic carbon (TOC),	[30]
Drought	100, 75, 50, 25% FC	A complex of 28 different species	*Bacillus* S48	-	Improvement of RWC Enhancement of proline content	[78]

Gabardi, S.; Douira, A.; Wahbi, S.; Outzourhit, A.; et al.et al. Arbuscular Mycorrhizal Fungi and/or Organic Amendment Enhance the Tolerance of Prickly Pear (Opuntia Ficus-indica) under Drought Stress. *J. Arid Environ.* **2022**, *199*, 104703, https://doi.org/10.1016/j.jaridenv.2021.104703.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
					Decrease in SOD, CAT, POX, and glutathione S-transferase (GST) Increase in soil EC	
Drought	Water regimes: 32 L/h for well-watered (WW); 16 L/h for drought stress (DS)	Aoufous consortium	PGPR consortium	Organic waste-based compost	Improvement of plant biomass Amelioration of plant-water relations Enhancement of P uptake A rise in total soluble sugar and protein content Decrease in MDA as well as H_2O_2 Improvement of soil traits,	[79]

44. Hussain, M.I.; Farooq, M.; Syed, Q.A.; Nutritional and Biological Characteristics of the Date Palm Fruit (Phoenix dactylifera L.)—A Review. *Food Biosci.* **2020**, *34*, 100509, https://doi.org/10.1016/j.fbio.2019.100509.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
					such as OM, P, and glomalin content	
Salinity	0, 50, 100, 200 mM NaCl	-	Endophytic bacteria	-	Ferric ion (Fe^{3+}) chelation, K^+ solubilization, phosphate ion (PO_4^{3-}) and zinc ion (Zn^{2+}), and ammonia (NH_3) production 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase together with IAA production capacity	[80]
Salinity	0, 240 mM NaCl	Aoufous consortium	-	-	Improvement of growth	[81]

55. Zein El Din, A.F.M.; Ibrahim, M.F.M.; Farag, R.; Abd El-Gawad, H.G.; El-Banhawy, A.; Alaraidh, I.A.; Rashad, Y.M.; Lashin, I.; Abou El-Yazied, A.; Elkelish, A.; et al.et al. Influence of Polyethylene Glycol on Leaf Anatomy, Stomatal Behavior,Water Loss, and Some Physiological Traits of Date

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
					and physiological traits Enhancement of water potential Amelioration of P, K as well as Ca content Decrease in MDA and H_2O_2 and rise in SOD, CAT, POX as well as APX activities	
Salinity	0, 240 mM NaCl	Aoufous consortium	-	Green waste-based compost	Amelioration of physiological parameters Improvement of P, potassium ion (K^+), and calcium ion (Ca^{2+}) content Enhancement	[82]

Salt-Susceptible Cultivars of Date Palm. *Agriculture* **2019**, *9*, 8, https://doi.org/10.3390/agriculture9010008.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
					of proline Reduction in the effect of lipid peroxidation and H_2O_2	
Salinity	Up to 7.6 dS m^{-1} NaCl	Identification of *Albahypha drummondii*, *Dominikia disticha*, *Funneliformis coronatus*, *Rhizoglomus irregular*	-	-	Positive correlation of soil salinity and intensity of mycorrhization Negative correlation of soil salinity and easily extractable glomalin	[83]
Salinity	0, 120, 240 mM NaCl	Aoufous consortium *Rhizophagus irregularis*	PGPR consortium	Green waste-based compost	Enhancement of growth traits and antioxidant defensive	[84]

...ctive. *Metabolites* **2020**, *10*, 505, https://doi.org/10.3390/metabo10120505.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
					machinery	
Salinity	0, 10, 20 g·L^{-1} NaCl	Autochthonous AMF Exogenous AMF	-	-	Negatively impacted growth as well as physiological properties	[85]
Heavy metal(oid)s	-	-	-	Organic manure	Enhancement of heavy metal(oid)s content in date palm fruits	[86]
Heavy metal(oid)s	$Pb(NO_3)_2$ 200 mg/L	*Glomus* spp.	*Rhizobium leguminosarum*	-	Improvement of root length, root fresh weight, shoot height, shoot fresh weight as well as the germination index Enhancement of seedling length, root basal diameter,	[87]

Mycorrhizal Fungi Complexes and Monospecific Isolates from Saline Semi-Arid Mediterranean Ecosystems Improved Phoenix dactylifera's Growth and Mitigated Salt Stress Negative Effects. *Plants* **2021**, *10*, 2501, https://doi.org/10.3390/plants10112501.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
					and dry biomass	
Heavy metal(oid)s	-	-	*Exiguobacterium* sp.	-	Identification of proteins/ enzymes involved in reducing heavy metal(oid)s contamination	[88]

Palm s.

scular in a Pb 7/978-3-

nd e

lar essed

dly Bio- Term Greenhouse Study in Northwestern Egypt. *J. King Saud Univ.-Sci.* **2022**, *34*, 102212, https://doi.org/10.1016/j.jksus.2022.102212.

7. AMF–PGPR Co-Inoculation and/or Organic Amendments

AMF, PGPR, and organic amendments constitute biological tools that hold tremendous potential to achieve sustainable agriculture. In addition, these environmentally friendly tools can assist the plants to withstand drought (**Figure 1**), salinity, and heavy metal(oid) (**Figure 2**) stresses. In this regard, available data corroborate the beneficial effects of biostimulants' co-inoculation on growth, as well as yield statuses of date palm under drought, salinity, and heavy metal(oid) constraints [89][90].

91. Bonini, P.; Rouphael, Y.; Miras-Moreno, B.; Lee, B.; Cardarelli, M.; Erice, G.; Cirino, V.; Lucini, L.; Colla, G.; Microbial-Based Biostimulant Enhances Sweet Pepper Performance by Metabolic Reprogramming of Phytohormone Profile and Secondary Metabolism. *Front. Plant Sci.* **2020**, *11*, 567388, https://doi.org/10.3389/fpls.2020.567388.

92. Mahanty, T.; Bhattacharjee, S.; Goswami, M.; Bhattacharyya, P.; Das, B.; Ghosh, A.; Tribedi, P.; Biofertilizers: A Potential Approach for Sustainable Agriculture Development. *Environ. Sci. Pollut. Res.* **2017**, *24*, 3315–3335, https://doi.org/10.1007/s11356-016-8104-0.

93. Sagar, A.; Rathore, P.; Ramteke, P.W.; Ramakrishna, W.; Reddy, M.S.; Pecoraro, L.; Plant Growth Promoting Rhizobacteria, Arbuscular Mycorrhizal Fungi and Their Synergistic Interactions to Counteract the Negative Effects of Saline Soil on Agriculture: Key Macromolecules and Mechanisms. *Microorganisms* **2021**, *9*, 1491, https://doi.org/10.3390/microorganisms9071491.

94. Khan, N.; Bano, A.; Ali, S.; Babar, M.A.; Crosstalk amongst Phytohormones from Planta and PGPR under Biotic and Abiotic Stresses. *Plant Growth Regul.* **2020**, *90*, 189–203, https://doi.org/10.1007/s10725-020-00571-x.

95. Masters-Clark, E.; Shone, E.; Paradelo, M.; Hirsch, P.R.; Clark, I.M.; Otten,W.; Brennan, F.; Mauchline, T.H.; Development of a Defined Compost System for the Study of Plant-Microbe Interactions. *Sci. Rep.* **2020**, *10*, 7521, https://doi.org/10.1038/s41598-020-64249-0.

96. Bulgari, R.; Franzoni, G.; Ferrante, A.; Biostimulants Application in Horticultural Crops under Abiotic Stress Conditions. *Agronomy* **2019**, *9*, 306, https://doi.org/10.3390/agronomy9060306.

97. Lephatsi, M.M.; Meyer, V.; Piater, L.A.; Dubery, I.A.; Tugizimana, F.; Plant Responses to Abiotic Stresses and Rhizobacterial Biostimulants: Metabolomics and Epigenetics Perspectives. *Metabolites* **2021**, *11*, 457, https://doi.org/10.3390/metabo11070457.

98. Devireddy, A.R.; Zandalinas, S.I.; Fichman, Y.; Mittler, R.; of Reactive Oxygen Species and Hormone Signaling during Abiotic Stress. *Plant J.* **2021**, *105*, 459–476, https://doi.org/10.1111/tpj.15010.

99. Bhoi, A.; Yadu, B.; Chandra, J.; Keshavkant, S.; Contribution of Strigolactone in Plant Physiology, Hormonal Interaction and Abiotic Stresses. *Planta* **2021**, *254*, 28, https://doi.org/10.1007/s00425-021-03678-1.

100. Saeed, W.; Naseem, S.; Ali, Z.; Strigolactones Biosynthesis and Their Role in Abiotic Stress Resilience in Plants: A Critical Review. *Front. Plant Sci.* **2017**, *8*, 1487, https://doi.org/10.3389/fpls.2017.01487.

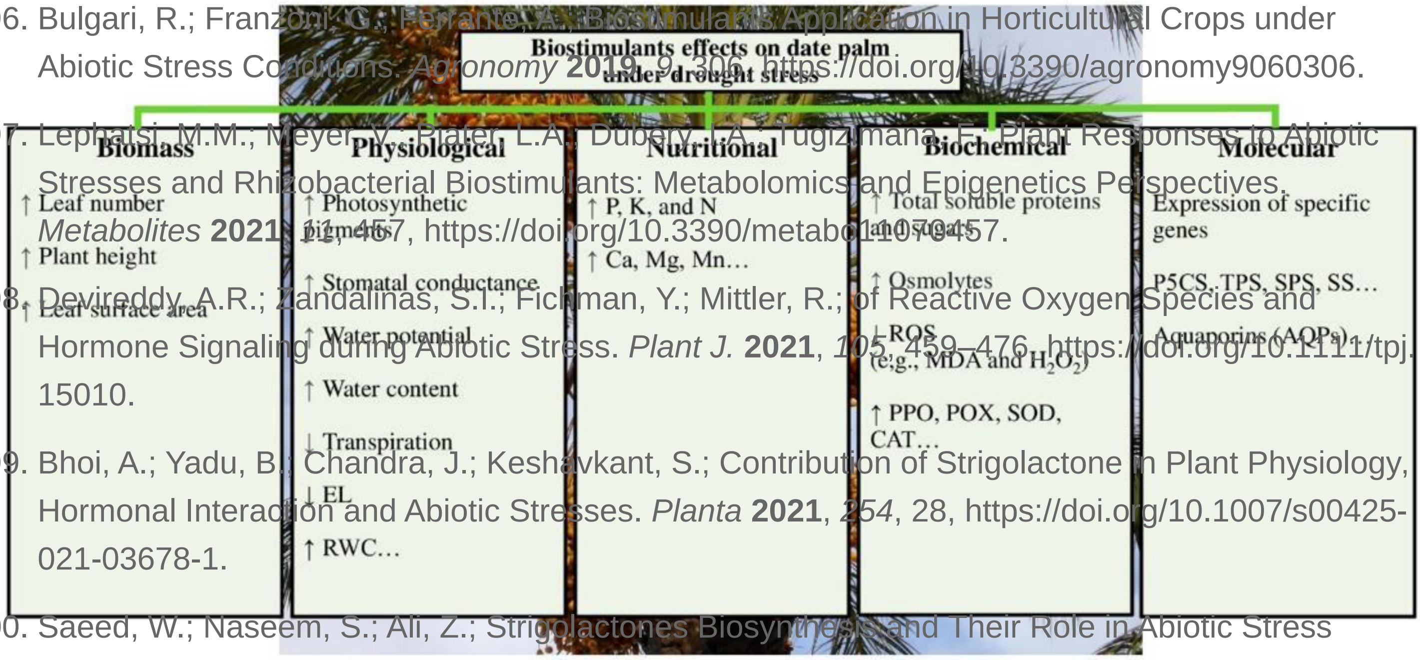

Figure 1. Effects of biostimulants on biomass, physiological, nutritional, biochemical, and molecular responses in date palm under drought stress. EL, electrolyte leakage; RWC, relative water content; ROS, reactive oxygen species; MDA, malondialdehyde; H_2O_2, hydrogen peroxide; PPO, polyphenol oxidase; POX, peroxidase; SOD, superoxide dismutase; CAT, catalase; P5CS, Δ1-Pyrroline-5-carboxylate synthase; TPS, Trehalose-6-phosphate synthase; SPS, sucrose-phosphate synthase; SS, starch synthase; AQPs, aquaporins; ↑, increase; ↓, decrease.

101. Fernández-Lizarazo, J.C.; Moreno-Fonseca, L.P.; Mechanisms for Tolerance to Water-Deficit Stress in Plants Inoculated with Arbuscular Mycorrhizal Fungi: A Review. *Agron. Colomb.* **2016**, *34*, 179–189, https://doi.org/10.15446/agron.colomb.v34n2.55569.

102. Bakshi, P.; Handa, N.; Gautam, V.; Kaur, P.; Sareen, S.; Mir, B.A.; Bhardwaj, R.; Role and Regulation of Plant Hormones as a Signal Molecule in Response to Abiotic Stresses. *Plant Signal. Mol. Role Regul. Stress. Environ.* **2019**, -, 303–317, https://doi.org/10.1016/B978-0-12-816451-8.00018-6.

103. Rehman, A.; Azhar, M.T.; Hinze, L.; Qayyum, A.; Li, H.; Peng, Z.; Qin, G.; Jia, Y.; Pan, Z.; He, S.; et al.et al. Insight into Abscisic Acid Perception and Signaling to Increase Plant Tolerance to Abiotic Stress. *J. Plant Interact.* **2021**, *16*, 222–237, https://doi.org/10.1080/17429145.2021.1925759.

104. Li, T.; Sun, Y.; Ruan, Y.; Xu, L.; Hu, Y.; Hao, Z.; Zhang, X.; Li, H.; Wang, Y.; Yang, L.; et al.et al. Potential Role of D-Myo-Inositol- 3-Phosphate Synthase and 14-3-3 Genes in the Crosstalk between Zea mays and Rhizophagus intraradices under Drought Stress. *Mycorrhiza* **2016**, *26*, 879–893, https://doi.org/10.1007/s00572-016-0723-2.

105. Tsukanova, K.A.; Chebotar, V.; Meyer, J.J.M.; Bibikova, T.N.; Effect of Plant Growth-Promoting Rhizobacteria on Plant Hormone Homeostasis. *S. African J. Bot.* **2017**, *113*, 91–102, https://doi.org/10.1016/j.sajb.2017.07.007.

106. Sami, F.; Faizan, M.; Faraz, A.; Siddiqui, H.; Yusuf, M.; Hayat, S.; Nitric Oxide-Mediated Integrative Alterations in Plant Metabolism to Confer Abiotic Stress Tolerance, NO Crosstalk with

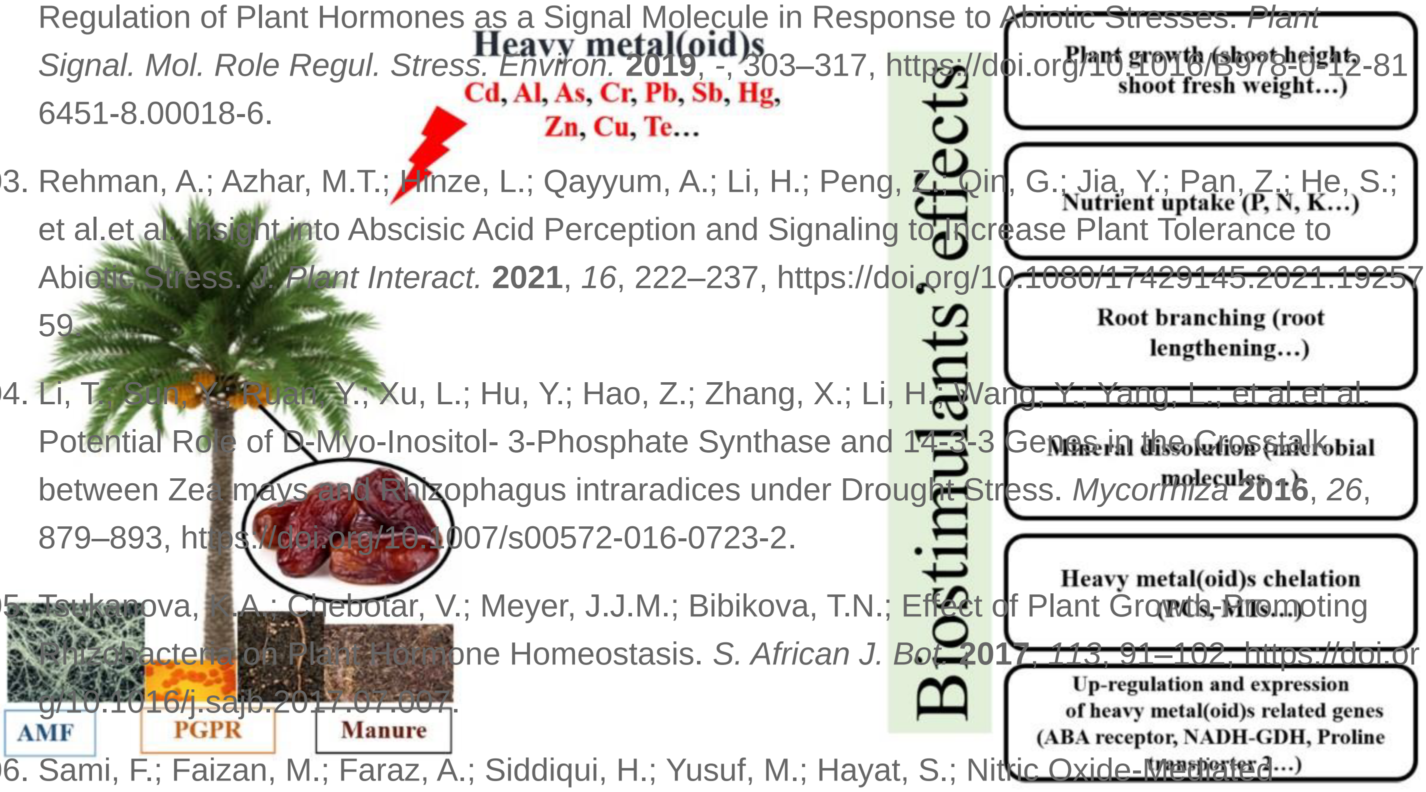

Figure 2. Detrimental effects of heavy metal(oid) and biostimulant roles in upgrading date palm fruits. Cd, cadmium; Al, aluminum; As, arsenic; Cr, chromium; Pb, lead; Sb, antimony; Hg, mercury; Zn, zinc; Cu, copper; Te, tellurite/tellurium; PCs, phytochelatins; MTs, metallothioneins; ABA, abscisic acid; NADH-GDH, NADH-glutamate dehydrogenase.

The performance improvement of date palm plants subjected to abiotic stresses can be attributed, in part, to the co-operation of AMF and PGPR and/or organic amendments. The co-inoculation of AMF together with PGPR improves the growth traits, total protein as well as soluble sugar content, plant nutrients, and antioxidant enzymes. Moreover, the beneficial biostimulants regulate plant hormones and modulate stress-related gene expression [91].

It remains to determine the microbial fraction and how each biostimulant's entity contributes to these beneficial effects. However, two main scenarios are possibly implicated:

- Strengthened in-common effects

The in-common effects of AMF–PGPR, plus compost or not, manifest through the mobilization and solubilization of P, improvement of K and N content, exudation of organic acids, soil stabilization, activation of the antioxidant defensive machinery, production and modulation of plant hormones, and soil enrichment in the organic matter [30] [79]. These crucial effects come under the umbrella of major roles played by biostimulants, executing biofertilizers, bioprotectors, biological control agents, and bio-effector effects (**Figure 3**). Biofertilizers essentially boost fertility and plant nutrition; bioprotectors work as biopesticides; biological control agents protect against pathogens; and bio-effectors modulate the plant's performance through direct/indirect patterns [29][92]. Thus, date palm plants treated with biostimulants can develop resilience to drought stress, salinity, and heavy metal(oid)s contamination, thanks to their improved robustness and immunization against abiotic stresses.

Phytohormones and NO-Mediated Post-Translational Modifications in Modulating Diverse Plant Stress. *Nitric Oxide-Biol. Chem.* **2018**, *73*, 22–38, https://doi.org/10.1016/j.niox.2017.12.005.

107. Ipek, M.; Mutluay, E.. Enhancing the Physiological and Molecular Responses of Horticultural Plants to Drought Stress through Plant Growth–Promoting Rhizobacterias; Elsevier: Amsterdam: The Netherlands, 2022; pp. 185–199.
108. Korver, R.A.; Koevoets, I.T.; Testerink, C.; Out of Shape During Stress: A Key Role for Auxin. *Trends Plant Sci.* **2018**, *23*, 783–793, DOI: https://doi.org/10.1016/j.tplants.2018.05.011.
109. He, J.; Xin, P.; Ma, X.; Chu, J.; Wang, G.; Gibberellin Metabolism in Flowering Plants: An Update and Perspectives. *Front. Plant Sci.* **2020**, *11*, 5–10, https://doi.org/10.3389/fpls.2020.00532.
110. Cortleven, A.; Leuendorf, J.E.; Frank, M.; Pezzetta, D.; Bolt, S.; Schmülling, T.; Cytokinin Action in Response to Abiotic and Biotic Stresses in Plants. *Plant. Cell Environ.* **2019**, *42*, 998–1018, https://doi.org/10.1111/pce.13494.
111. Prakash, V.; Singh, V.P.; Tripathi, D.K.; Sharma, S.; Corpas, F.J.; Nitric Oxide (NO) and Salicylic Acid (SA): A Framework for Their Relationship in Plant Development under Abiotic Stress. *Plant Biol.* **2021**, *23*, 39–49, https://doi.org/10.1111/plb.13246.
112. Wang, Y.; Mostafa, S.; Zeng, W.; Jin, B.; Function and Mechanism of Jasmonic Acid in Plant Responses to Abiotic and Biotic Stresses. *Int. J. Mol. Sci.* **2021**, *22*, 8568, https://doi.org/10.3390/ijms22168568.
113. Bleecker, A.B.; Kende, H.; Ethylene: A Gaseous Signal Molecule in Plants. *Annu. Rev. Cell Dev. Biol.* **2000**, *16*, 1–18, https://doi.org/10.1146/annurev.cellbio.16.1.1.
114. Husain, T.; Fatima, A.; Suhel, M.; Singh, S.; Prasad, S.M.; Singh, V.P.; A Brief Appraisal of Ethylene Signaling under Abiotic Stress in Plants. *Plant Signal. Behav.* **2020**, *15*, 1782051, https://doi.org/10.1080/15592324.2020.1782051.

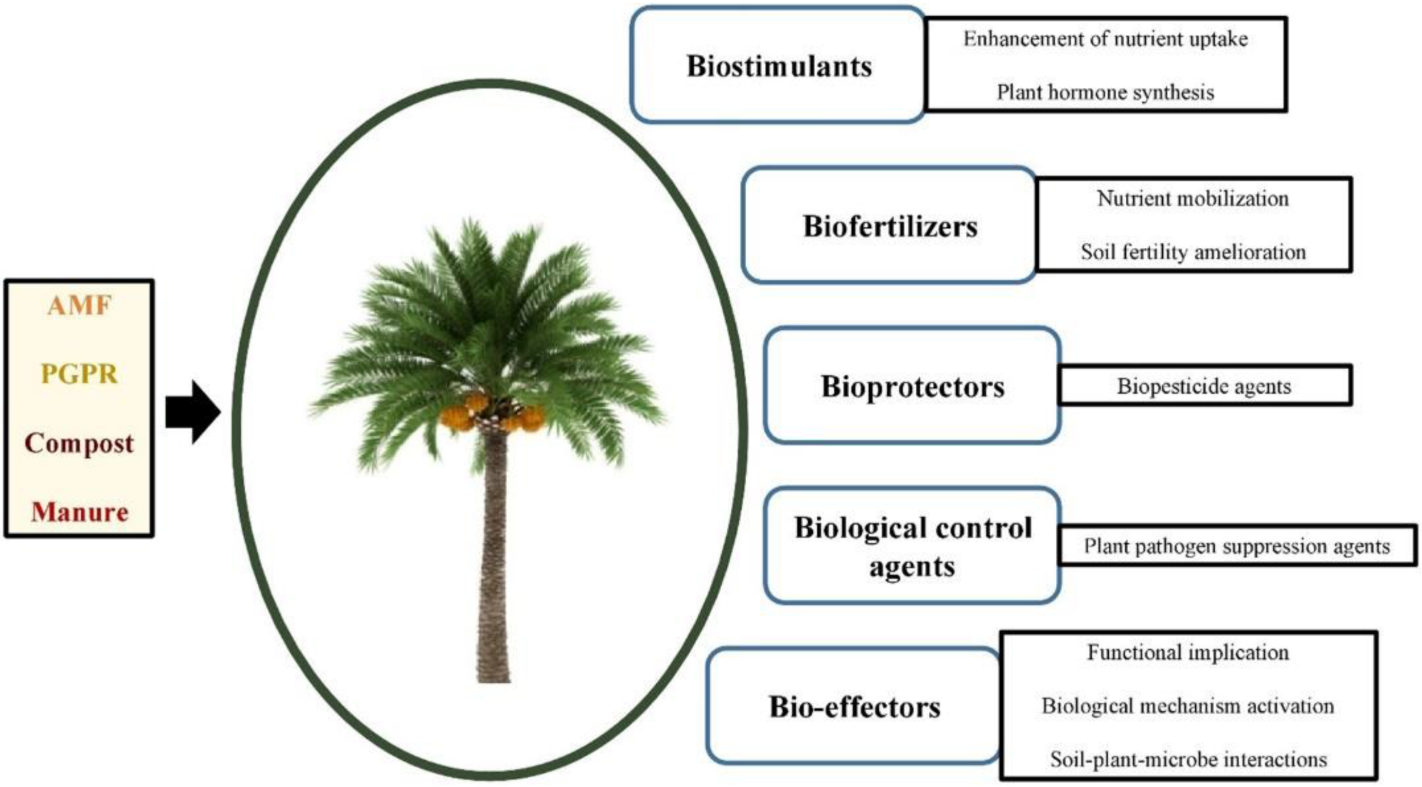

Figure 3. Different roles played by AMF, PGPR, and organic amendments in date palm plants' resilience to environmental stressors.

- Synergistic and complementary effects

The synergistic and complementary effects of AMF–PGPR and/or compost (and manure) are probably the result of each biostimulant when combined. AMF produce glomalin-related soil protein (GRSP), a mycelia glycoprotein that mainly boosts the soil's organic carbon storage and structure aggregation, and heavy metal(oid) toxicity reduction. Furthermore, AMF improve water uptake and nutrient assimilation, thanks to ameliorating absorption surface area by mycorrhizal hyphae. Finally, AMF interact with and modulate aquaporin (AQP) gene expression. Mycorrhizae can modify the plant's roots' hydraulic conductivity, probably via regulating AQP gene expression [93].

PGPR can form polysaccharides-based biofilms, thus allowing the host plant to perceive stimuli related to changing environmental conditions, such as temperature and pH. Another attribute of PGPR is exopolysaccharides (EPS) enhancement, which protects against desiccation. Siderophores represent iron-chelating agents that PGPR secrete and can assure sequestration effects. Some PGPR can secrete ACC-D. The enzyme is involved in the cleavage of ethylene's precursor, which is a crucial step in attenuating its concentrations and assuring plant growth. In addition, PGPR produce antibiotics that can enhance the plant's growth traits, lytic enzymes, such as cellulases, glucanases, proteases, and chitinases, and some bacterial strains can even fixate N_2 and enhance nitrate (NO^{3-}) assimilation [94].

The application of compost and manure has the advantage of assuring water retention, thanks to the component of humus, diversification of microbial biomass, fertility effects, and availability of (macro-)micro-elements. Humus as a crucial component of both compost and manure can help sustain moisture and water going through plants' roots [95].

8. Biostimulants and Plant Hormones: Initiating and Suppressing Effects

Biostimulants have been gaining momentum in the world of agriculture, thanks to their remarkable roles in combatting the detrimental consequences of abiotic stresses [96]. Biostimulants' application can lead to either initiating or suppressing date palm's growth processes, hence ameliorating productivity under environmental and biotic constraints. In this regard, biostimulants play major roles in the upregulation and downregulation of plant hormones [97].

Specific responses are co-ordinated by signaling molecules, such as plant hormones. Abiotic stresses lead to excessive ROS production. In response to ROS-generated oxidative stress, plant hormones intervene to achieve resilience by modifying the plant's omics patterns [98].

8.1. AMF–Plant Hormones

AMF act by regulating the physiological processes of plants, which enhances their productivity and product quality. As a reaction to abiotic stresses, the plant–AMF association leads to plant hormones, as well as signaling molecules, production. Therefore, plants' functional processes, such as nutrient and water cycling, are efficiently maintained [99].

Mycorrhizal plants secrete strigolactones (SLs) upon the perception of abiotic stresses. As relatively newly discovered plant hormones, SLs enact majorly in rhizospheric communication, germination, as well as seed growth stimulation, shoot branching regulation, and inducement of the AMF hyphae branching [100]. Furthermore, SLs can improve the hydration profile and RWC in mycorrhizal plants, for instance [101].

Another prominent plant hormone is ABA, which is denominated as the stress plant hormone. ABA's concentration can remarkably be enhanced within mycorrhizal plants in response to abiotic stressors [102][103]. It was observed that activating 14-3-3 protein and aquaporins (GintAQPF1 and GintAQPF2) within *Rhizophagus intraradices* was mediated by the concurrent expression's enhancement of plant genes encoding for D-myo-inositol-3-phosphate synthase (IPS) and 14-3-3-like protein GF14 (14-3GF) that are responsible for the transduction of ABA signaling. These findings highlight that IPS and 14-3GF co-expression may be the triggering factor in AMF–plant's synergistic effects, as per resilience to abiotic stresses [104].

8.2. PGPR–Plant Hormones

PGPR interaction is assured through quorum-sensing molecules that control gene expression pathways and plant hormone synthesis. They interact closely alongside the root system of higher plants, influencing the tenor of endogenous plant hormones. Therefore, PGPR offer a novel concept for hormonal interaction [105].

Auxins (IAA), gibberellins (GAs), and cytokinins (CKs) are plant regulators that are produced in extremely low concentrations. However, they exert a significant impact on plants' physiological and biochemical activities under abiotic stresses [106]. PGPR can secrete IAA, GAs, and CKs in response to environmental constraints [107].

Indole-3-acetic acid or IAA represents the most naturally occurring form of auxins. IAA accumulation leads to the regulation of the stomatal aperture. At the guard cells level, H_1-ATPase-associated movements within the cell membrane are regulated by IAA. H_1 efflux stimulates K_1 influxion, adjusted by the hyperpolarized membrane potential. Abiotic stresses lead to accumulating a significant amount of the plant hormone, leading to a restriction of K_1 influxion against its effluxion, eventuating in the *closing* of stomata [102][108].

GAs intervene in cell expansion and transitioning from vegetative to reproductive growth [109]. GAs act against abiotic stresses. For instance, when plants are subjected to salt stress, DELLA (aspartic acid–glutamic acid–leucine–leucine–alanine) proteins that are negative regulators of the GA signaling pathway become stabilized, as they over-accumulate due to decreased bioactive GA.

CKs represent a class of plant hormones that act through cytokinesis, cell division, as well as apical dominance regulators. As plants become exposed to drought and salt stresses, CK levels start to decline at the level of xylem sap via downregulation of specific isopentenyl transferase (IPT) genes. Generally, isoprene-type CKs, such as tZ and tZ riboside, would decrease following abiotic stresses, such as water deficit. *Arabidopsis* histidine kinases (AHK) CK receptors, more precisely AHK2 and AHK4, can be downregulated in the process of tolerating abiotic stresses [110].

Salicylic acid (SA) constitutes a plant hormone that derives from the shikimate–phenylpropanoid pathway. It is a phenolic plant hormone that is implicated in several processes related to the plant's growth but acts against environmental constraints as well, mainly by regulating stomatal opening [111].

Jasmonates (JAs) occur naturally as fatty acids that comprise jasmonic acid (JA), among other compounds, such as methyl jasmonate and JA–isoleucine conjugate. The structure of JA is 3-oxo-2-20-cis-pentenyl-cyclopentane-1-acetic acid and it is regarded as a stress-induced plant hormone. When plants are subjected to drought stress, JA intervenes by reducing the loss of water and regulating the stomatal aperture's opening. TFs like ZIM (zinc-finger inflorescence meristem)-domain proteins (JAZ) act as regulators under water scarcity. On the other hand, leaves' growth can be inhibited due to the accumulation of JA in response to salinity. In addition, JA helps increase the concentrations of antioxidative compounds, as well as antioxidant enzymatic activities [112].

Ethylene (ET) is an unsaturated alkene hydrocarbon and a gaseous molecule that works like a plant hormone, which controls many developmental as well as metabolic processes within plants [113]. ET can act as a stress hormone during abiotic stress events. The ET signaling pathway modulates the downstream of the constitutive triple response1 (CTR1) regulator and is dependent on ROS. APETALA2/ET responsive factors (AP2/ERFs) are TFs that play a crucial part in downstream ethylene signaling [114], which contributes to attenuating abiotic stresses.