




Review

Biostimulants as Innovative Tools to Boost Date Palm (*Phoenix dactylifera* L.) Performance under Drought, Salinity, and Heavy Metal(Oid)s' Stresses: A Concise Review

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Abstract: Date palm (*Phoenix dactylifera* L.) is constantly subjected to abiotic stresses. Hence, the application of biostimulants, such as the arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR), and organic amendments hold tremendous potential to significantly improve the growth and yield of date palm. 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, in addition to molecular modulation. In this regard, the present concise review focuses on highlighting the beneficial impact of AMF and PGPR, as well as the organic amendments, in boosting the health status and productivity of date palm plants subjected to abiotic stresses. Furthermore, mechanisms reinforcing date palm plants' resilience to abiotic stresses, powered by biostimulants, are particularly emphasized. Based on this review, we could conclude that the overall findings corroborate the beneficial effects of AMF-PGPR and/or compost and manure application in terms of boosting date palm's growth traits, development, yielding, as well as soil properties under extreme environmental factors, such as those of drought, salinity, and excessive heavy metal(oid)s. Thus, biostimulants can confer resilience to date palm plants against abiotic stresses.

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



Citation: Akenous, F.-Z.; Anli, M.; Meddich, A. Biostimulants as Innovative Tools to Boost Date Palm (*Phoenix dactylifera* L.) Performance under Drought, Salinity, and Heavy Metal(Oid)s' Stresses: A Concise Review. *Sustainability* **2022**, *14*, 15984. <https://doi.org/10.3390/su142315984>

Academic Editors: Fanrong Zeng, Imran Haider Shamsi and Xin Huang

Received: 30 October 2022

Accepted: 25 November 2022

Published: 30 November 2022

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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, which 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 affect the leaf size, extension of stems, proliferation of roots, and water-plant relations [16–18]. 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 CO₂ 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 our 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 ecofriendly 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 are played by PGPR; they can fix nitrogen (N), solubilize phosphorus (P), decrease heavy metal(oid) pollution, produce plant hormones, mineralize the organic matter in soils, and provide resilience to abiotic stresses [31,34]. Furthermore, compost constitutes the final product of organic material decomposition [35]. Compost assures several beneficial effects; it essentially serves as a growth medium, an organic fertilizer, a soil amendment, and a water-retaining ameliorator [36]. 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 [37].

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.

In the recent past, many reviews attempted to highlight the role of beneficial microbes' communities in enhancing the resilience profile of date palm plants in response to drought stress and salinity, such as the review work of Hazzouri et al. [38]. Moreover, many case studies were surveyed concerning biostimulants' effects in improving several crops' growth traits and productivity, as well as resilience to abiotic stressors [4,39]. However, the impact of AMF, PGPR, and/or organic amendments, especially their combined application, on date palm's overall performance under abiotic stresses has rarely been highlighted through a review. Thus, the novelty and main objective of the present concise review consist in underscoring recent available data regarding AMF, PGPR, and/or organic amendments (compost and manure) on growth traits, physiological properties, biochemical parameters, as well as molecular features within date palm subjected to abiotic stresses, particularly drought stress, salinity, and heavy metal(oid) pollution.

The present concise review was constructed based on relevant peer-reviewed, selected case studies, carried out during the last five years (2017–2022), relying on proven research platforms and engines like SciVerse Scopus, SCIE-SSCI/Web of Science, and Google Scholar. The combined items used throughout the review's research process included: "date palm abiotic stresses", "date palm drought", "date palm salinity", "date palm heavy metals", "date palm AMF", "date palm PGPR", "date palm compost", and "date palm genes".

2. History and Distribution of Date Palm

Probably, date palm might be the oldest plant in the world [40], 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 [41]. 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 [42].

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 [40].

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 [40,41]. Date palm holds an important socio-economic value amongst leading countries growing the crop for its most appreciated fruits: the dates [43,44]. 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 [45]. 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 [46].

4. Pests, Diseases, and Anthropogenic Constraints

Date palm is continuously subjected to biotic stresses, with insects and fungi being the main causal agents [46,47]. *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 [48], 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 [49]. Additionally, date palm plants are often infested with *Ceratocystis paradoxa* and *C. radicola*, two fungal species that can distress about any part of the plant [50].

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 [40,43].

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

Drought stress, salinity, and heavy metal(oid) pollution count as aggressive environmental factors to plants such as *P. dactylifera*. 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 enviroining 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 plants' cellular, molecular, and metabolic functioning [51].

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 A rise in total phenolic compounds, peroxidase (POX), polyphenol Amelioration of (PPO) activities A rise in calcium (Ca), iron (Fe), and zinc (Zn)	[52]
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	[53]
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, 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	[54]
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 (WUE _i)	[55]
Drought	Gradual decline in humidity	Plantlets	"Sewi"	Dehydration A decline in photosynthetic pigments Decline in surviving chances	[56]

Table 1. Cont.

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	[57]
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 response, photosynthesis, and antioxidant-related proteins Downregulation of gene expression, metabolic, and secondary metabolism-related proteins	[25]
Drought	50, 100, 150% of evapotranspiration levels	Trees	"Succary"	A decline in date palm yielding Affected fruit traits An overall decline in fruit metabolites	[58]
Drought	50, 75, 100% of watering demand	Trees	"Khalas"	Affected fruit yielding as well as quality	[59]
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 in photosynthetic properties	[60]
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	[61]

Table 1. Cont.

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
Salinity	5, 10, 15 dS m ⁻¹ of salt water	Trees	“Ajwat AlMadinah”, “Naghal”, “Khniizi”, “Barhi”, “Makhtoumi”, “Farad”, “Khisab”, “Nabtat-Saif”, “Shagri”, “Abu-Maan”, “Jabri”, “Sukkari”, “Rothan”	Excluding of Na ⁺ Retaining of K ⁺ Decease in osmotic potential	[62]
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	[63]
Salinity	50, 300 mM NaCl	Seedlings	“Khalas”	Decease in photosynthetic capacity, stomatal conductance (gs), rate of transpiration (E), and root system traits Hypermethylated and hypomethylated DNA regions, coupled with insignificant genes expression	[64]
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	[65]
Salinity	0, 240 mM NaCl	Seedlings	“Umsila”, “Zabad”	A decline in leaf fresh and dry weights	[66]
Salinity	0, 300 mM NaCl	Seedlings	“Khalas”	Decrease in leaf area, leaf and root dry weights, K ⁺ accumulation, and roots’ Casparian strips Enhancement of stress-related metabolites (e.g., osmolytes and antioxidant enzymes)	[67]

Table 1. Cont.

Abiotic Stress	Stress Level	Growth Stage	Cultivar/Variety	Main Effects	References
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)	[68]
Salinity	<1, 12–15, 18–20 dS m ⁻¹ of saline water	4-year-old trees	-	A decline in actual water use	[69]
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)	[70]
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	[61]
Salinity	5, 10, 15 dS m ⁻¹ of salt water	Trees	“Ajwat Al Madinah”, “Naghal”, “Barhi”, “Shagri”, “Abu Maan”, “Jabri”, “Sukkari”, “Rothan”, “Khinizi”, “Maktoumi”	Increase in minerals, mainly K, P, and Ca	[62]
Salinity	Irrigation levels based on crop evapotran- spiration (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	[58]
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]

Table 1. Cont.

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 (<i>pcs</i>) and metallothionein (<i>mt</i>) 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 surpassed the maximal allowable levels (MAL)	[74]

5.1. Drought

Drought is an abiotic stressor that constitutes a major threat to date palm. Drought stress is governed by factors such as the dynamics of temperature and precipitation/rainfall. Its impact is multidimensional, as it severely affects plants’ biomass, physiological, nutritional, biochemical, and molecular profiles (Figure 1). Thus, the plant’s yielding potential is often negatively impacted in terms of overall performance and product quality [75].

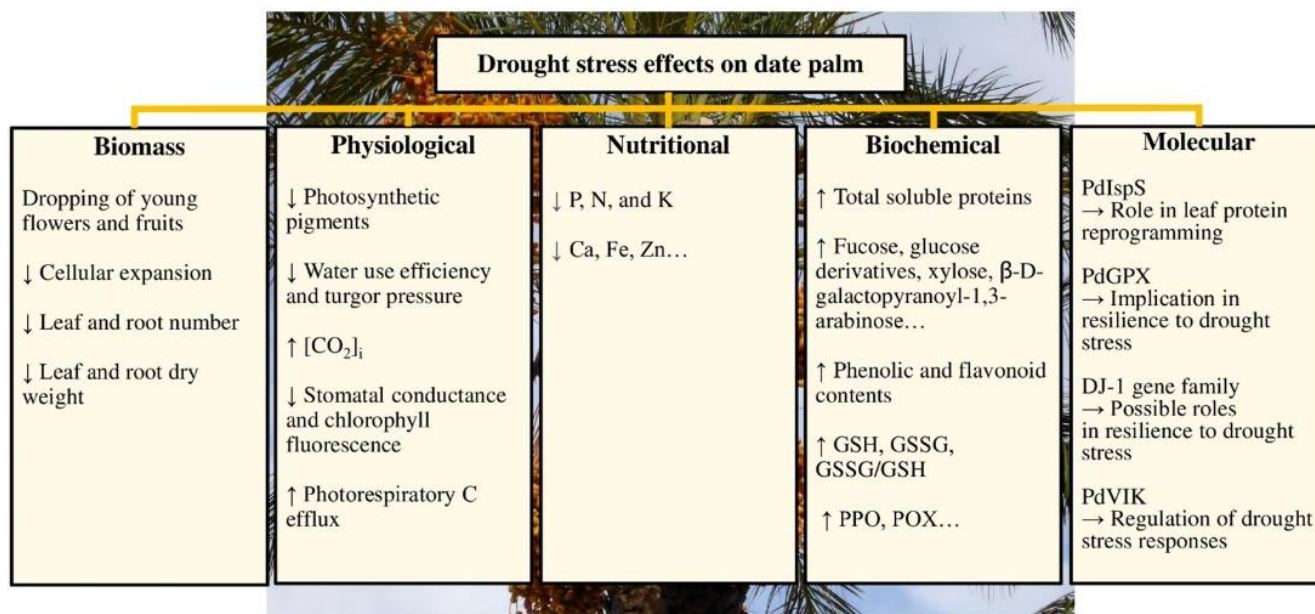


Figure 1. Effects of drought on biomass, physiological, nutritional, biochemical, and molecular traits in date palm. GSH, reduced glutathione; GSSG, oxidized glutathione; PPO, polyphenol oxidase; POX, peroxidase; PdIspS, isoprene synthase; PdGPX, glutathione peroxidase gene family; DJ-1, protein deglycase; PdVIK, vascular highway 1-interacting kinase.

Alikhani-Koupaei et al. [52] noted that water limitations negatively affected the growth performance of date palm plants aged 10–12 years old, belonging to the “Mazafati” variety. Such effects are often manifested by the dropping of young flowers and fruits during flowering and fruit setting phases. It was suggested that fruit cellular expansion is more sensible to water limitations than its cellular division. Moreover, cell growth can be blocked, owing to low turgor pressure. In another study carried out by [76], the authors observed that leaf and root numbers, in addition to leaf and root dry weights, were significantly affected by decreasing water potential in date palm’s 4–5-year-old female offshoots of the “Barhee”, “Ruziz”, and “Sukary” cultivars. Probably, biomass decline helps the uptake of water by date palm plants under water deficit.

Drought stress exerts negative consequences on date palm plants’ physiological traits. The authors of [76] observed that water-use efficiency (WUE), relative water content (RWC), and photosynthetic capacity were severely affected by water limitations in the “Barhee”, “Ruziz”, and “Sukary” cultivars. However, the internal carbon dioxide concentration $[CO_2]_i$ increased within date palm offshoots. The $[CO_2]_i$ evolution under water deficit may indicate the insufficiency of CO_2 use throughout photosynthesis. Furthermore, the decrease in photosynthetic capacity may be attributed to stomatal closure and metabolism impairment. Water deprivation led to a substantial decline in leaf hydration and net CO_2 assimilation in date palm plants aged 1–2 years old [25,57]. Under drought, photorespiration intervenes as a vital tactic in attenuating drought stresses’ detrimental effects, though it may result in $1/3$ loss of the photosynthetic C fixation. This is in corroboration with a study highlighting signals of induced photorespiratory C efflux within the leaves of date palm plants subjected to summer-like climate conditions [77]. Moreover, heat and drought occurring episodes may intensify photorespiration and photosynthesis competition, which corroborates the reduced rate of assimilation and stomatal conductance in date palm plants under drought [55].

Nutrient availability, as well as uptake, can usually be hampered under drought conditions. A study conducted by [52] revealed that leaf calcium (Ca), iron (Fe), and zinc (Zn) content were reduced under deficit irrigation in date palm plants aged 10–12 years old, belonging to the “Mazafati” variety, and with a history of bunch wilting. Mineral assimilation depends on water availability, as water flow and path are critical for mineral uptake from the soil to the root system. For instance, water deficit can lead to an increased concentration of hydroxide (OH), which can obstruct Fe assimilation control in roots.

Drought-induced biochemical changes have been extensively documented in date palm. The authors of [17] recorded enhanced fucose and glucose derivatives in date palm seedlings due to water limitations. However, [57] observed that, except for raffinose, many sugars, mostly β -D-galactopyranosyl-1,3-arabinose and xylose, declined under water deficit conditions. Carbohydrates are believed to act as osmoprotectants of plant cells against drought-induced oxidative stress. On the other hand, [57] observed that drought resulted in a substantial decline in ascorbate tenor. Moreover, water deficit conducted to a significant accumulation of individual leaf amino acids, such as β -alanine, within date palm seedlings.

Secondary metabolism is triggered by drought stress. This was evidenced in 3-month-old date palm seedlings of the “Sagie” cultivar [53]. Drought led to changes in the phenolic and flavonoid content. Total reduced glutathione (GSH), glutathione disulfide (GSSG), as well as GSSG/GSH ratio considerably increased [57]. Under such conditions, soil water content (SWC) and isoprene emissions decreased substantially as well. Thus, it was suggested that isoprene emission patterns were implicated in isoprene biosynthesis, which can help date palm leaves cope with heat and/or drought stresses. Nonenzymatic antioxidants’ accumulation acts as an effective ROS scavenging method in response to osmotic tension, enabling date palm plants to survive under drastic conditions of water deficit [52]. Furthermore, enzymatic antioxidants, such as peroxidase (POX) and polyphenol oxidase (PPO), were enhanced with drought severity and exposure period.

Drought was also shown to induce changes on the molecular level within date palm plants. In a study conducted by [25], a prominent result was identifying and functionally

characterizing the gene that encodes for *P. dactylifera* isoprene synthase (PdIspS). The gene plays a key role in reprogramming leaf-related protein profiles, which leads to date palm plants' resilience to water deficit under extreme temperatures of summer. Moreover, a study relative to the genetic profile of date palm revealed the identification of five *P. dactylifera* glutathione peroxidase (PdGPX) genes implicated in resilience to drought. Date palm PdGPX genes are phylogenetically matching other glutathione peroxidases (GPX)-related genes that were previously identified in monocot species [28]. In another study, it was suggested that characterizing the glyoxalase III (DJ-1) gene family's function could provide additional insights into its responsive role under drought stress [67]. It has recently also been demonstrated that *P. dactylifera* vascular highway 1-interacting kinase (PdVIK), which represents an MAPK kinase kinase (MAPKKK) gene, is involved in regulating drought stress responses of date palm plants [64].

5.2. Salinity

Soil and water salinity represent major threats to date palm plants. Salinity impairs plants' growth, mainly due to water deficit and the assimilation of ions such as sodium (Na^+) and chloride (Cl^-). Consequently, plants are prone to severe oxidative stress and nutritional imbalance [78]. The authors of [28] observed that the leaf area, as well as leaf and root dry masses, were negatively affected in date palm seedlings of the "Khalas" cultivar exposed to salinity. Available data support the conclusion that salinity reduces date palm yield characteristics in terms of quantity and quality, probably due to detrimental effects on reserve translocation during the fruiting period [79].

Water-plant relations and vital physiological functions are altered under salinity in date palm plants. Salinity affects the ability of date palm to absorb water due to the osmotic impact and alteration in cell-water relations [76]. Moreover, it exerts a detrimental impact on photosynthetic pigments [80,81]. Several studies, however, found that, when salinity increased, the content of chlorophyll considerably decreased [66,76]. One of the prompt date palm's reactions to salinity is stomatal closure, which results in a decrease in photosynthetic capacity [82]. The loss of chloroplast membranes, extreme swelling, and the development of lipid droplets may be responsible for the salinity-induced decrease in chlorophyll concentration [65].

Mineral assimilation status plays a major role in date palm plants' overall performance. Yet, the uptake of Na^+ and Cl^- ions hampers the plants' mineral assimilation [65,82,83]. Na^+ is the most detrimental ion because it prevents K^+ from being absorbed and disturbs a variety of activities, such as stomatal control.

In a study carried out by [61] on date palm seedlings of the "Deglet Nour" cultivar, the authors recorded a substantial drop in soluble proteins against an enhancement in the total soluble protein content. On the other hand, they noted varied catalase (CAT) and superoxide dismutase (SOD)-related activities with exposure period to salinity.

A total of 319 significant metabolite features were predicted within date palm seedlings of the "Deglet Nour" variety [61]. For instance, the mass-to-charge ratio (m/z) 739.4266 feature was maximized and then decreased in response to higher salinity. In addition, the feature 552.40's concentration augmented with salinity and the period of exposure, with a total absence of the feature at $0 \text{ g L}^{-1} \text{ NaCl}$.

Moreover, 25 predicted and identified metabolites were found to belong to molecule classes such as terpenoids, phenols, vitamins, and lipids, indicating secondary metabolite enhancement with salinity and time exposure. The biosynthesis of secondary metabolites, which attenuates the salt stress effects through ROS scavenging, is possibly adjusted to excess salinity within a succinct evolutionary time interval.

5.3. Heavy Metal(Oid)s

The pollution of the soils and water with heavy metal(loid)s accounts for a huge risk to date palm, essentially due to the toxicity factor that leads to major functional alterations. The detrimental effects are manifested at the nutritional and biochemical levels especially.

In a study carried out by [74], arsenic (As), antimony (Sb), and cadmium (Cd), followed by aluminum (Al), chromium (Cr), and lead (Pb) concentrations were substantially high in date palm fruits belonging to the “Kadary”, “Safawy”, “Eklas”, “Barney”, “Rashadya”, “Sakay Normal”, “Mabroum”, and “Sakay” varieties. The dates at maturity and ripening stages, when polluted with heavy metal(oid)s in excess, can represent huge risks for the consumer that range from degeneration of brain cells to kidney and bone damage. On the other hand, [84] recorded a significant decrease in P, potassium (K), Ca, as well as magnesium (Mg) tenor within roots, together with shoots in date palm seedlings of the “Khalas” variety. Cd is acknowledged to impair the uptake and transportation of nutritional elements, which can lead to a considerable imbalance in metabolic activities. Furthermore, Cd stress enhanced malondialdehyde (MDA) levels, as well as POX and catalase (CAT) activities. Probably, ROS led to the disturbance of membrane integrity and, consequently, its injury under heavy metal(oid) stress, which is counteracted by the antioxidant enzymes.

Heavy metal(oid)s led to alterations in plant hormones. Absciscic acid (ABA), jasmonic acid (JA), as well as salicylic acid (SA) were enhanced within date palm subjected to Cd stress. Endogenous ABA plays a crucial role in regulating different physiological processes. In addition, it acts as a regulator of the stomatal aperture opening. As a consequence, it positively affects WUE and operates as an efficient modulator of date palm’s metabolism under heavy metal(oid) contamination [85].

In their attempt to assess molecular mechanisms implied in the detoxification of Cd and Cr within date palm plants, [73] tracked the expression of phytochelatin synthase (*Pdpcs*) and metallothionein (*Pdmt*) genes by generating sequences for candidates and housekeeping genes (HKGs) belonging to “Deglet Nour” variety. The findings revealed that *Pdpc* and *Pdmt*’s gene expression was reduced or suppressed with metal concentration. Consequently, these results indicated that both investigated genes were involved in detoxifying heavy metal(oid)s, as their expression profile might be controlled at the transcriptional phase in date palm under Cd and Cr stresses. Therefore, changes in *Pdmt* and *Pdpc*’s gene expression could serve as prompt-signal biomarkers of heavy metal(oid) stress within date palm.

In another study conducted by [27], the authors assessed putative genes controlling some important agronomic traits, such as the phosphatidyl inositol signaling system, phosphatase activity, and alternative enzyme pathways related to the biodegradation of xenobiotics, secondary metabolism, phenyl propanoid biosynthesis, in addition to glutathione metabolism in date palm explants of the “Deglet Nour” variety. In addition, real-time polymerase chain reaction (qPCR) data indicated that the expression of cytosolic copper (Cu)/Zn-superoxide dismutase (Cu/Zn SOD) was substantially downregulated under Cd stress. Nevertheless, the ABA receptor pyrabactin-like (PYL4)’s expression manifested an important upregulation. Transcript overaccumulation of ABA biosynthesis genes can trigger the degenerative process of leaf senescence. As a consequence, this can lead to impaired photosynthesis functioning, thereby repressing date palm’s growth performance and productivity under heavy metal(oid)s contamination [84].

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 [86,87]. Available data corroborate the positive impact of biostimulants on date palm, especially in terms of resilience to abiotic stress [88] (Table 2).

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

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
Drought	75, 25% FC	<i>Rhizoglossus irregulare</i> 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 ₂ O 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	<i>Bacillus</i> S48	-	Improvement of RWC Enhancement of proline content Decrease in SOD, CAT, POX, and glutathione S-transferase (GST) Increase in soil EC	[89]
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 ₂ O ₂ Improvement of soil traits, such as OM, P, and glomalin content	[90]
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	[91]

Table 2. Cont.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
Salinity	0, 240 mM NaCl	Aoufous consortium	-	-	Improvement of growth and physiological traits Enhancement of water potential Amelioration of P, K as well as Ca content Decrease in MDA and H ₂ O ₂ and rise in SOD, CAT, POX as well as APX activities	[82]
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 of proline Reduction in the effect of lipid peroxidation and H ₂ O ₂	[80]
Salinity	Up to 7.6 dS m ⁻¹ NaCl	Identification of <i>Albahypha drummondii</i> , <i>Dominikia disticha</i> , <i>Funneliformis coronatus</i> , <i>Rhizoglyphus irregular</i>	-	-	Positive correlation of soil salinity and intensity of mycorrhization Negative correlation of soil salinity and easily extractable glomalin	[92]
Salinity	0, 120, 240 mM NaCl	Aoufous consortium <i>Rhizophagus irregularis</i>	PGPR consortium	Green waste-based compost	Enhancement of growth traits and antioxidant defensive machinery	[81]
Salinity	0, 10, 20 g·L ⁻¹ NaCl	Autochthonous AMF Exogenous AMF	-	-	Negatively impacted growth as well as physiological properties	[93]
Heavy metal(oid)s	-	-	-	Organic manure	Enhancement of heavy metal(oid)s content in date palm fruits	[94]
Heavy metal(oid)s	Pb(NO ₃) ₂ 200 mg/L	<i>Glomus</i> spp.	<i>Rhizobium leguminosarum</i>	-	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, and dry biomass	[95]

Table 2. Cont.

Abiotic Stress	Level of Stress	Biostimulants			Main Effects	References
		AMF	PGPR	Organic Amendment		
Heavy metal(oid)s	-	-	<i>Exiguobacterium</i> sp.	-	Identification of proteins/enzymes involved in reducing heavy metal(oid)s contamination	[96]

6.1. AMF

6.1.1. Drought

In a study conducted by [30], the authors observed that growth traits, particularly the leaf number, plant height, and leaf area, were improved in date palm seedlings of the “Bouffgous” variety subjected to drought, thanks to inoculation with *Glomus monosporus*, *G. clarum*, and *G. deserticola*. AMF protect the photosynthetic apparatus of date palm under water limitations. Mycorrhizal date palm plants responded with high water potential levels and higher water content, leading to maintenance of high organ hydration and turgor levels (=cell integrity), despite water deficit. Water uptake enhancement and/or transpiration decrease could be pronounced in mycorrhizal date palm plants. Furthermore, it was suggested that mycorrhizal date palm seedlings could display alterations in cell wall elasticity and water redistribution between apoplastic and symplastic compartments. On this basis, date palm inoculated with AMF can exhibit a better ability to overcome drought stress, thanks to positive effects on physiological attributes, such as stomatal conductance, electrolyte loss/leakage (EL), and RWC [30,90,97,98].

The inoculation with AMF can improve plants’ nutrient use efficiency, which can be explained by a better surface uptake or assimilation, provided through extended fungal hyphae [99]. This is in line with the findings of [100], who recorded an important content of P, Ca, Mg, K, and manganese (Mn) within mycorrhizal date palm seedlings belonging to the “Bouffgous” variety.

It was demonstrated that AMF’s input leads to the enhancement of sugar and protein content under drought stress. Moreover, mycorrhizal date palm plants exhibit high antioxidant enzyme activities, PPO and POX, for instance [30,90]. PPO catalyzes the formation of quinones involved in cell wall stiffness and resilience to abiotic stresses. Furthermore, the accumulation of osmolytes and reinforcement of the antioxidant machinery can be implicated in osmotic adjustment, cell turgor maintenance, protection of cell structures, and scavenging of ROS (e.g., hydrogen peroxide (H₂O₂) and MDA). Suggestively, the minimal lipid peroxidation damage in mycorrhizal date palm plants could be due to a primary drought avoidance strategy as well. AMF–date palm association led to the regulation of water uptake through triggering hormonal signaling, such as ABA that mediates stomatal conductance [98].

6.1.2. Salinity

Date palm plants colonized by AMF manifest amelioration in growth traits, notably the plant’s height, leaf area, and root density, in addition to plant fresh and dry weights under saline conditions. Thus, AMF–date palm association leads to more biomass production [101]. The notable amelioration in date palm growth traits was attributed to the better uptake of nutrients [82].

AMF-assisted enhancement of the photosynthetic pigment content, such as chlorophyll, has been reported in date palm plants subjected to salinity [81,82]. According to these studies, AMF enhanced the uptake of minerals, especially, Mg which represents the major center of the chlorophyll molecule [65]. Furthermore, photosynthetic capacity was enhanced in AMF–date palm plants, thanks to an increase in gas exchange capacity,

photosystem II (PS II) efficiency, and regulation of the energy flow between photochemical and nonphotochemical reactions [82]. The net assimilation rates' amelioration, assured by the PS II photochemical machinery protection and the rise in stomatal conductance under salinity, is probably a result of resilience to salinity [102].

Another beneficial attribute of AMF is the retraction of Na^+ coming out of the xylem, as well as its diversion through the photosynthetic tissues to the roots of date palm, being the host plant. Hence, the toxic effects of Na^+ in the apoplasm remain minimal compared to the cytoplasm [103,104].

Mycorrhizal date palm exhibited higher SOD, CAT, and POX activities under salinity [80,82]. The important capacity of ROS scavenging can be attributed to AMF boosting the antioxidant machinery. The high activity of these enzymes in mycorrhizal date palm plants reduced the oxidative damage, with less accumulation of MDA and H_2O_2 [81,82]. Indeed, AMF possess various oxidative stress-related genes (e.g., SOD genes). When upregulated, these genes contribute to reinforcing date palm plants' resilience to environmental stresses, such as salinity [105].

AMF-assisted date palm plants can regulate salinity-related genes. For instance, mycorrhizal symbiosis upregulates genes encoding for Na^+ and K^+ transporters, such as ZmAKT2, ZmSOS1, and ZmSKOR, responsible for maintaining the K^+/Na^+ homeostasis in roots [106]. These transporters promote Na^+ extrusion from the cytoplasm and sequestration into vacuoles, resulting in improved salt tolerance. Furthermore, a study effectuated by [107] revealed that, out of 12 reference genes, 18S ribosomal RNA (18S), YT521, SMALL SUBUNIT RIBOSOMAL RNA (25S), as well as ubiquitin (UBQ), ELONGATION FACTOR 1-ALPHA and ACTIN were stable within leaves and roots of date palm plants subjected to salinity.

6.1.3. Heavy Metal(Oid)s

Inoculation with AMF plays an important role in boosting date palm plants' growth under heavy metal(oid)s contamination. Yet, AMF effects highly depend on factors such as mycorrhizal isolates, plant species, and implicated heavy metal(oid)s [108]. The authors of [95] investigated the capacity of isolates from AMF, *Glomus* spp. (A01), and PGPR, *Rhizobium leguminosarum* (GM01), for phytoremediation and dealing with Pb uptake by date palm. Overall, date palm plants treated with the combination of A01 and GM01 exhibited better growth traits and biomass accumulation by enhancing the root length, root fresh weight (RFW), shoot fresh weight (SFW), shoot height, and germination index. It was suggested that AMF contribute synergistically by improving the uptake of nutrients, branching patterns of roots, as well as transformation and detoxification of Pb [109].

AMF engage in the uptake of soil's heavy metal(oid)s to the plant through their extraradical mycelium at the level of the fungal plasma membrane [110,111]. Furthermore, AMF can produce specific enzymes that degrade xenobiotic contaminants, making AMF-assisted phytoremediation a promising means of remediation for contaminated soils. Therefore, resilience to heavy metal(oid) contamination can be established by AMF through several strategies, such as compartmentation, intracellular sequestration, complexation, extracellular precipitation and sequestration, volatilization, and cell-wall binding of heavy metal(oid)s [111,112].

Heavy metal(oid)s contamination can indeed be attenuated by AMF through several mechanisms:

- Heavy metal(oid)s biofortification/phytoextraction, as AMF improve date palm's growth traits, water status, and P assimilation, which decreases heavy metal(oid)s through the dilution effect. These roles are facilitated thanks to the mycorrhizal pathway that involves high-affinity metal transporters located at the extraradical mycelium of the symbiotic interface (root hairs and epidermal cells) [112–114].
- Phytostabilization, as AMF lead to the immobilization and sorption of heavy metal(oid)s (e.g., Mn, Zn, Cu, Fe, and cesium (Cs)) in mycorrhizal date palm plants, specifically in the level of extra-radicular mycelium structures. Moreover, mycorrhizae bind heavy

metal(oid)s against the cell wall, chelate metallic ions within the cytosol, and facilitate their compartmentalization in the vacuoles by stabilizing them with polyP [113,115].

- Detoxification through the antioxidant defense machinery activation (e.g., SOD) [116].
- Overexpression of protective proteins in the level of mycorrhizal roots (e.g., heat-shock proteins and glutathione transferase) [116].
- Exudation of organic acids, which contributes to the reduction in metal mobility in the soil, in addition to chelation by glomalin [117].

6.2. PGPR

6.2.1. Drought

PGPR can boost date palm plants' growth and performance even under a water deficit. Probably, date palm plants can grow better despite water limitations, if an improved nutritional status is provided [118]. In a study carried out by [30], autochthonous PGPR strains contributed to improving date palm seedlings' growth of the "Boufeggous" variety, thanks to the uptake enhancement of low-mobility nutrients, such as P and N. Growth traits, such as shoot height, leaf surface, shoot dry weight (SDW), and SFW, were also substantially improved within date palm vitroplants of the "Boufeggous" variety, grown under field conditions, thanks to the application of a local PGPR consortium [90]. Moreover, physiological and biochemical properties, such as chlorophyll fluorescence, stomatal conductance, photosynthetic pigments, and osmolytes, were all bacteria-enhanced. On the other hand, ref. [89] noted that PGPR contributed to decreasing the leaf's CAT activity in seedlings of date palm subjected to severe water stress. PGPR contribute to attenuating the effects of drought stress by modifying the root system, implying the root's architecture, depth, angle, density, volume, and biomass. In addition, PGPR assist in modulating genes' expression in response to stress, producing phytohormones, osmolytes, siderophores, volatile organic compounds (VOC), and exopolysaccharides, as well as enhancing 1-aminocyclopropane-1-carboxylate (ACC) deaminase activities [119].

6.2.2. Salinity

PGPR have been reported for ameliorating the productivity of plants subjected to saline conditions [120]. Salinity affects the growth, physiological, nutritional, and biochemical parameters of date palm plants. Nevertheless, PGPR application contributes to improving these traits. In a study conducted by [81], PGPR-assisted date palm vitroplants belonging to the "Boufeggous" variety showed improvement in the plants' height and SDW, osmoprotectants, and antioxidant defensive machinery, thereby leading to osmotic adjustment and resilience to salinity. On the other hand, [121] isolated and sequenced the genome of *Microbacterium* sp. Strain Yaish 1 from date palm groves affected with salinity. The authors identified growth-promoting ACC deaminase (ACC-D), siderophore-producing proteins, and tryptophan biosynthesis protein-coding genes. Hence, available data suggest the effectiveness of PGPR growth-boosting mechanisms that can confer resilience to date palm plants against salinity.

6.2.3. Heavy Metal(Oid)s

PGPR can effectively mitigate date palm plants' contamination with heavy metal(oid)s. The authors of [95] noted that the inoculation with *Rhizobium leguminosarum* proved to positively influence date palm's growth traits, notably the root length, root fresh weight, shoot height, as well as shoot fresh weight, in addition to an improved germination index. The authors suggested that PGPR help with nutrient availability, pathogen suppression, and root branching enhancement in date palm.

The regulation of heavy metal(oid)s-related genes is assisted through PGPR application. The genome sequencing of a bacterial strain, *Exiguobacterium* TNDT2, isolated from an Indian date palm rhizosphere, revealed the presence of Arsenate reductase (EC 1.2.0.4.1); As, Pb, Cd, Zn, and mercury (Hg)-transporting ATPase (EC 3.6.3.3) (EC 3.6.3.5); Cu-translocating P-type ATPase (EC 3.6.3.4); Cobaltzinc-cadmium resistance protein CzcA;

Anion permease ArsB/NhaD-like; Mercuric ion reductase (EC 1.16.1.1); Cd-transporting ATPase (EC 3.6.3.3); Camphor resistance CrcB protein; Tellurite resistance protein, as well as the quaternary ammonium compound resistance protein SugE. These enzymes are mainly implicated in the chelation and mineral dissolution of insoluble phases [96].

6.3. Organic Amendments

6.3.1. Drought

Organic amendments' application can promote date palm plants' performance under drought stress. In response to water limitations, the organic amendments can improve physiological attributes, such as chlorophyll and carotenoid concentrations, relative water content, leaf water potential, and stomatal conductance in date palm [30,90]. Probably, the organic amendments provide minerals such as N, P, K, and Mg, which are crucial for chlorophyll production [122–124]. Therefore, organic fertilizers impact date palm's growth processes that lead to chloroplast and chlorophyll production, as well as chloroplast enzyme activity, thus ameliorating the photosynthetic activity under water limitations [125]. It appears plausible to speculate that chlorophyll content enhancement may be attributed to more important levels of N, K, Mg, and Ca, which are vital components of the chlorophyll molecule and necessary for its production [126–128].

The moderate application of compost can boost date palm plants' performance and assist in their resilience to drought stress, thanks to ameliorated mineral nutrient uptake and soil enrichment in an accessible nutrient reservoir, particularly soils poor in organic matter, as evidenced in date palm [30,90].

Leaf soluble carbohydrates, proteins, and proline content increased in date palm plants assisted with organic amendments. Organic fertilizers were proven to induce the buildup of osmolytes, helping in drought stress alleviation [30]. This suggests that biostimulants promote the buildup of organic osmolytes, resulting in decreased osmotic potentials within date palm host cells in response to water deficit.

The impact of organic amendments on the resilience status to drought stress via date palm's defensive machinery, particularly the antioxidant aspect, is rarely investigated [30,90]. Available data indicate that date palm plants subjected to water limitations and treated with organic amendments exhibit a substantial increase in the activities of antioxidant enzymes, such as SOD, POX, CAT, and PPO. Furthermore, organic amendments contribute to reducing MDA and H₂O₂, as well as EL [30,129]. Overall, date palm develops resilience to drought stress thanks to the improvement of cell membrane integrity and flexibility and reinforced antioxidant defense machinery through the organic amendments' input [123,130–132].

6.3.2. Salinity

The addition of organic amendments, such as compost, can substantially improve soil's physical, chemical, as well as biological parameters. Consequently, date palm plants' growth traits can be strengthened even under salinity [80–82]. Compost enhances these features, thanks to attributes such as nutrient availability, improved soil structure, and/or increased soil water content.

Furthermore, the application of compost can improve gas exchange, and, thereby, photosynthesis, in plants grown under salinity. According to a case study about date palm plants grown under salt stress, organic amendments improved growth traits by increasing the stomatal conductance and density. Moreover, the authors observed an increase in transpiration, suggesting that evaporation decline and a higher soil organic matter could be the main involved factors [82].

On the other hand, compost improved date palm plants' resilience to salinity by intrigued biosynthesis of proteins, chlorophyll-containing compounds, and enhanced P and N uptake [81]. Moreover, it was shown that compost contributes to maintaining appropriate K⁺/Na⁺ and Ca²⁺/Na⁺ ratios and a lower pH, thus providing date palm plants with the necessary minerals and nutrients [82].

6.3.3. Heavy Metal(Oid)s

The application of organic manure can be a suitable biological alternative, which can boost date palm plants' growth status, as well as yield under heavy metal(oid) contamination. In a study carried out by [94], nutritional content, mainly N, P, K, Ca, Mg, Fe, Zn, Mn, and Cu, have substantially improved within date palm fruits of the "Khenazi" cultivar. Thus, organic manure probably acts as a nutrient reservoir and an organic matter enhancer, which contributes to attenuating heavy metal(oid) contamination. Moreover, the authors recorded an amelioration in fruit and flesh weights, total soluble solids (TSS) of fruit volume, and moisture content. Probably, the input of organic manure can improve date palm fruits' nutritional content and yield under heavy metal(oid) pollution.

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 2), salinity, and heavy metal(oid) (Figure 3) 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 [133,134].

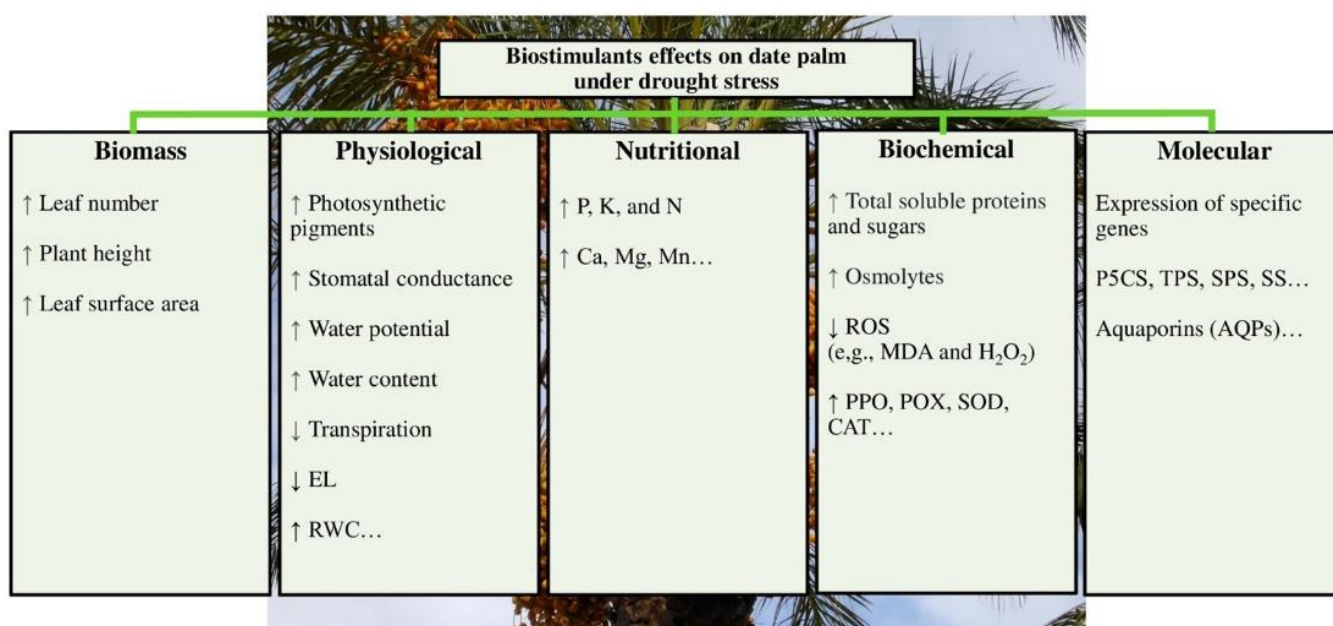


Figure 2. Effects of biostimulants on biomass, physiological, nutritional, biochemical, and molecular responses in date palm under drought stress. EL, electrolyte leakage; RWC, relative water content; ROS, reactive oxygen species; MDA, malondialdehyde; H₂O₂, hydrogen peroxide; PPO, polyphenol oxidase; POX, peroxidase; SOD, superoxide dismutase; CAT, catalase; P5CS, Δ 1-Pyrroline-5-carboxylate synthase; TPS, Trehalose-6-phosphate synthase; SPS, sucrose-phosphate synthase; SS, starch synthase; AQPs, aquaporins; ↑, increase; ↓, decrease.

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, beneficial nutrients, and antioxidant enzymes. Moreover, the beneficial biostimulants regulate plant hormones and modulate stress-related gene expression [135].

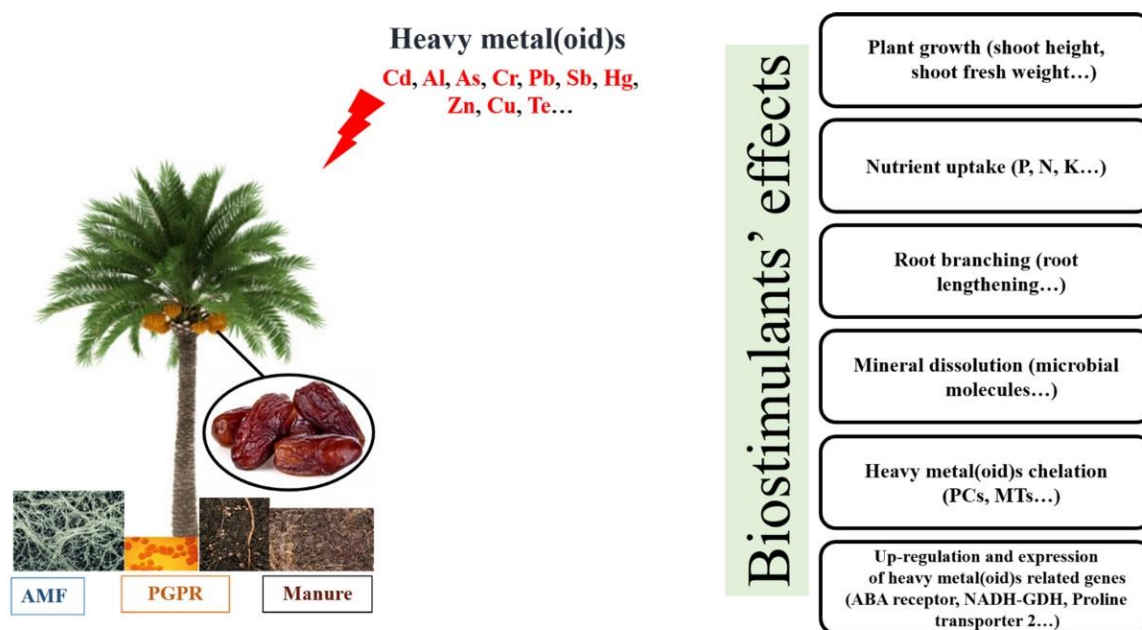


Figure 3. Detrimental effects of heavy metal(oid) and biostimulant roles in upgrading date palm fruits. Cd, cadmium; Al, aluminum; As, arsenic; Cr, chromium; Pb, lead; Sb, antimony; Hg, mercury; Zn, zinc; Cu, copper; Te, tellurite/tellurium; PCs, phytochelatin; MTs, metallothioneins; ABA, abscisic acid; NADH-GDH, NADH-glutamate dehydrogenase.

It remains to determine the microbial fraction and how each biostimulant's entity contributes to these beneficial effects. However, two main scenarios are probably 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 [30,90]. These crucial effects come under the umbrella of major roles played by biostimulants, executing biofertilizers, bioprotectors, biological control agents, and bio-effector effects (Figure 4). 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 [29,136]. Thus, date palm plants treated with biostimulants can develop resilience to drought stress, salinity, and heavy metal(oid) contamination, thanks to the improved robustness and immunization against abiotic stresses.

- Synergistic and complementarity 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 [137].

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 [85].

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 and can help sustain moisture and water going through plants' roots [138].

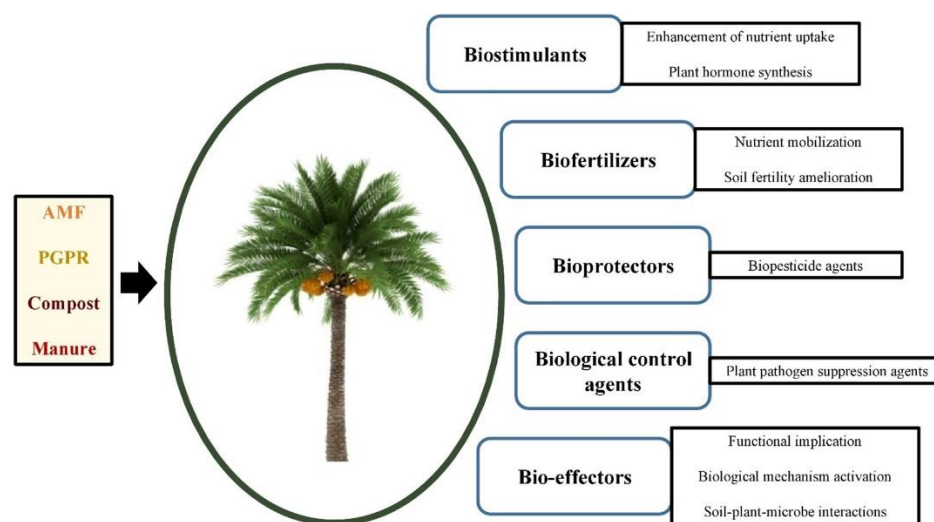


Figure 4. Different roles played by AMF, PGPR, and organic amendments in date palm plants' resilience to environmental stressors.

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 [139]. 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 [140].

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 [141].

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 hormone, as well as signaling molecule, production. Therefore, plants' functional processes, such as nutrient and water cycling, are efficiently maintained [142].

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 [143]. Furthermore, SLs can improve the hydration profile in plants, RWC in mycorrhizal plants, for instance [144].

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 [145,146]. 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), which 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 [147].

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 [148].

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 [149]. PGPR can secrete IAA, GAs, and CKs in response to environmental constraints [150].

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, H₁-ATPase-associated movements within the cell membrane are regulated by IAA. H₁ effluxion stimulates K₁ influxion, adjusted by the hyperpolarized membrane potential. Abiotic stresses lead to accumulating a significant amount of the plant hormone, leading to a restriction of K₁ influxion against its effluxion, eventuating in the *closing* of stomata [145,151].

GAs intervene in cell expansion and transitioning from vegetative to reproductive growth [152]. 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 a 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 [153].

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 [154].

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 such as 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 [155].

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 [156]. 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 reactive oxygen species (ROS). APETALA2/ET responsive factors (AP2/ERFs) are TFs that play a crucial part in downstream ethylene signaling [157], which contributes to attenuating abiotic stresses.

9. Research Gaps

According to available data, biostimulants such as AMF, PGPR, and organic amendments play crucial roles in date palm plants' resilience to abiotic stresses. In addition, these eco-friendly means hold tremendous potential in enhancing date palm plants' overall performance and yield under drastic environmental stressors, notably drought, salinity, and heavy metal(oid)s.

Nevertheless, information regarding the exact mode of action of every single biostimulant is uncertain. Furthermore, the exact fraction by which every biostimulant contributes to building resilience to abiotic stresses is yet to be investigated. Other important aspects to determine are the optimal dose precisions, opportune time application, and exact formulations, as well as accurate methods of inoculation. AMF and PGPR species and strains vary with environmental conditions and respond accordingly, which implies that the biological biostimulants are species-specific. Thus, available information on one biostimulant cannot be extrapolated to another. Moreover, it is difficult to determine the share of each microbial (AMF and or PGPR) and organic (compost and manure) fraction and their interactions within the tripartite combination performing to enhance date palm's resilience to abiotic stresses.

Available data offer suggestive information on how date palm plants possibly withstand abiotic stresses, thanks to the potential benefic effects of biostimulants. Yet, investigation on the molecular and omics levels is critical to determine the exact operating modes. For all the above-mentioned reasons, available data in the literature can further be confirmed through extensive molecular investigation, at the omics level, applying computer science tools and advanced features. Moreover, there is a crucial need for models that can assess date palm–biostimulant interactions, taking into consideration the fact that date palm is a pseudo-trunk, often categorized as a tree.

10. Conclusions and Perspectives

Owing to climate change, together with global warming, climate events are intensifying, which is affecting plants' performance and productivity on a regional and global scale. Date palm is no exception, since its growth and yield are often hampered due to prolonged episodes of drought stress, salinity, and heavy metal(oid)s contamination. As a result, date palm plants' production has been disturbing over the years. Thus, an integrative approach towards both sustainable agriculture and quality production is crucial to boosting the phoeniculture sector. In this regard, biostimulants can offer a plethora of benefits. Available data suggest probable synergistic and complementary effects of the co-inoculation with AMF–PGPR and/or organic amendments' application. Nevertheless, further research is needed to confirm these effects.

Additionally, plant hormones play critical roles in signaling and commending accurate responses to environmental stresses. However, plant regulators' effects on date palm plants are yet to be explored. Thanks to advances in high-throughput genotyping technologies, knowledge about functional genomics and molecular genetics can help figure out the exact functioning of plant hormones, as well as their cross-talk signaling pathways in date palm, in response to abiotic stresses. Therefore, improving the understanding of these research areas could bring insights into how date palm plants develop resilience to abiotic stressors and by which means the composition of biostimulants helps fasten the process.

In pursuance of this ultimate goal, which is a thorough examination of the multi-beneficial roles played by the studied biostimulants, in-field trials are strongly required to provide insights that could confirm and consolidate the accuracy of available data from greenhouse and controlled growth chamber experiments. Furthermore, modeling date palm–biostimulant interactions under open field conditions, using artificial intelligence, the internet of things, and machine learning technologies is a promising futuristic outlook that can significantly advance our understanding in this regard.

Author Contributions: Conceptualization, A.M. and M.A.; software, F.-Z.A., M.A. and A.M.; writing—original draft preparation, F.-Z.A. and M.A.; writing—review and editing, F.-Z.A., M.A., and A.M.; visualization, F.-Z.A., M.A. and A.M.; supervision, A.M.; project administration, A.M. and M.A. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Tuniso-Moroccan Mixed Laboratories (LMTM) of Plant Physiology and Biotechnology and Climate Change LPBV2C (LR11ES09).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

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