Crop Drought Tolerance: Strategies and Improvements

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Drought: A Global Threat

Meteorological Drought

Reduction in rain fall supply compared with a specified average condition, less than a certain amount ***e.g.* 70%**

Agricultural Drought

Reduction in water availability below the optimal level required by a crop at different growth stage, resulting in impaired growth and reduced yields

Hydrological drought

The impact of a reduction in precipitation on natural and artificial surface and sub-surface water resources

Socio-economic drought

Direct and indirect impact of drought on human activities

Plant Drought Resistance Mechanisms

Can be broadly grouped into:

✓**Avoidance**

OR

✓**Tolerance**

Drought avoidance mechanisms associated with:

Physiological whole-plant mechanisms such as:

- Canopy resistance
- Leaf area reduction (decrease radiation adsorption and transpiration)
- Stomatal closure
- Cuticular wax formation (reduce water loss)
- Adjustments to sink-source
- Allocations through altering root depth and density, root hair development, and root hydraulic conductance

Drought tolerance mechanisms

Generally those that occur at the cellular and metabolic level involved in:

- Turgor maintenance
- Protoplasmic resistance
- Dormancy
- Altering the expression of a complex array of genes

Physiological, biochemical and molecular processes affected by drought stress

- Synthesis of photosynthetic pigments
- Photosynthesis
- Respiration
- Accumulation of reactive oxygen species (ROS)
- Vital membranes leakage/damage
- Activity/level of enzymes involved in metabolism
- Uptake/accumulation of essential inorganic nutrients
- Biosynthesis/Transportation of plant growth regulators
- Regulation (up or down) of genes

All these drought-induced changes directly or indirectly affect plant growth and development as well as expression of different genes involved therein

DROUGHT STRESS

Physiological Responses

- Recognition of root signals
- Loss of turgar and osmotic adjustment
- Reduced leaf water potential (ψ)
- Decrease in stomatal conductance to CO_2
- Reduced internal CO_2 concentration
- Decline in net photosynthesis
- Reduced growth rates

Biochemical Responses

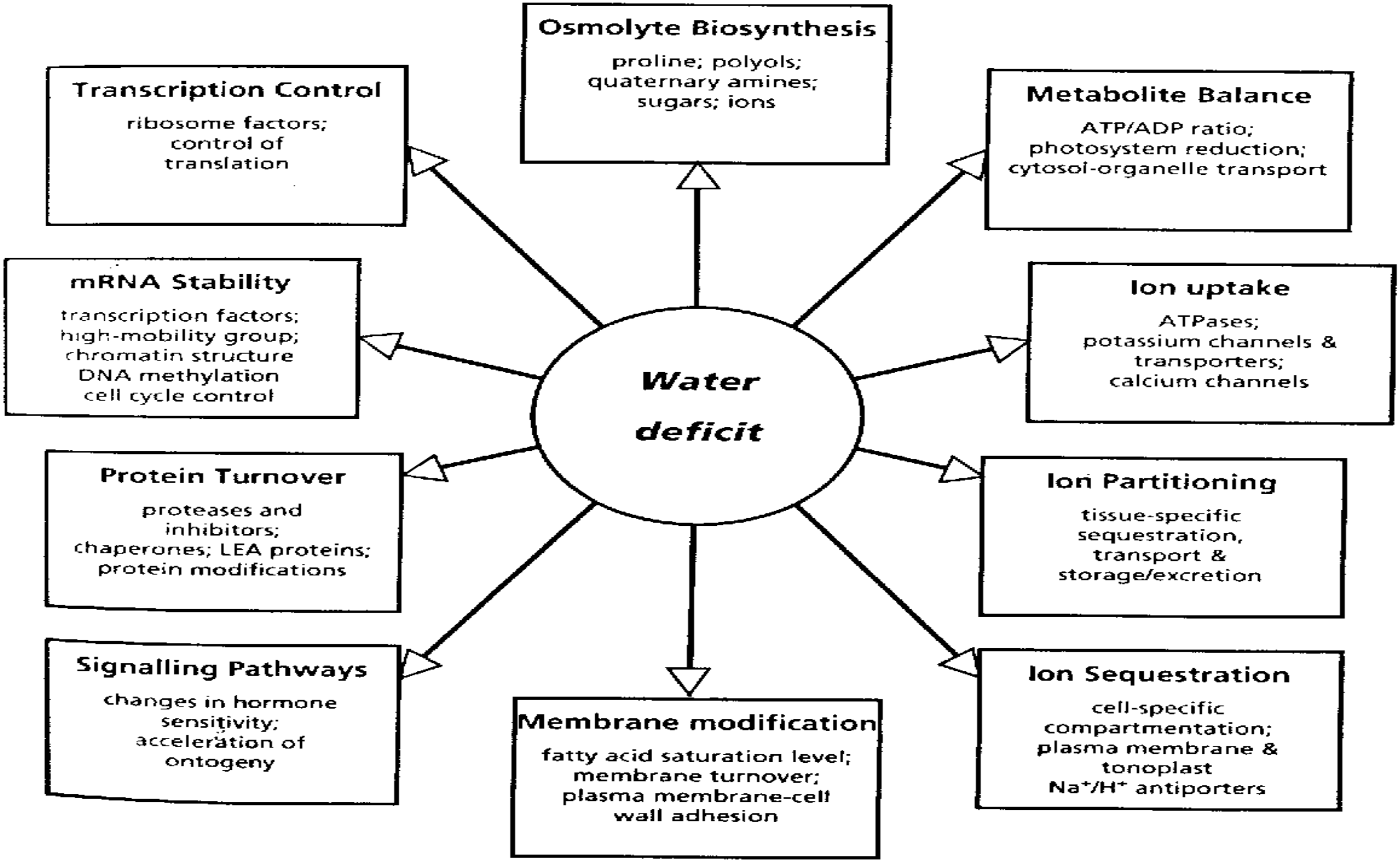
- Transient decrease in photochemical efficiency
- Decreased efficiency of Rubisco
- Accumulation of stress matabolites like MDHA, Glutathione, Pro, Glybet, Polyamines, and ∝-tocopherol
- Increase in antioxidative enzymes like, SOD, CAT, APX, POD, GR and MDHAR
- Reduced ROS accumulation

Molecular Responses

- Stress responsive gene expression
- Increased expression in ABA biosynthetic genes
- Expression of ABA responsive genes
- Synthesis of specific proteins like LEA, DSP, RAB, dehydrins
- Drought stress tolerance

Shao et al., 2008

General Modulations under Water Stress



Water deficit

Transcription Control
ribosome factors;
control of
translation

Osmolyte Biosynthesis
proline; polyols;
quaternary amines;
sugars; ions

Metabolite Balance
ATP/ADP ratio;
photosystem reduction;
cytosol-organelle transport

mRNA Stability
transcription factors;
high-mobility group;
chromatin structure
DNA methylation
cell cycle control

Ion uptake
ATPases;
potassium channels &
transporters;
calcium channels

Protein Turnover
proteases and
inhibitors;
chaperones; LEA proteins;
protein modifications

Ion Partitioning
tissue-specific
sequestration,
transport &
storage/excretion

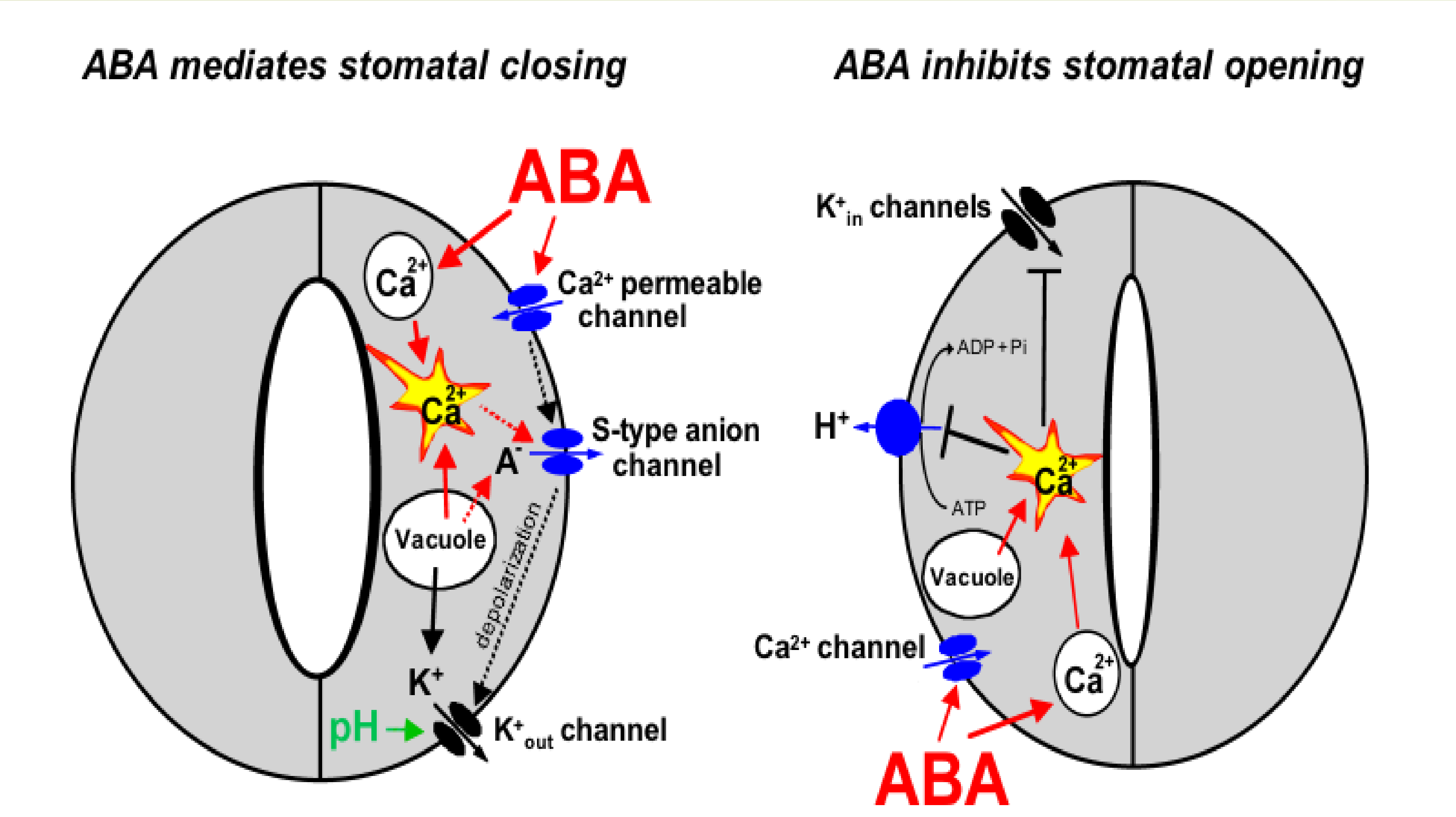
Signalling Pathways
changes in hormone
sensitivity;
acceleration of
ontogeny

Membrane modification
fatty acid saturation level;
membrane turnover;
plasma membrane-cell
wall adhesion

Ion Sequestration
cell-specific
compartmentation;
plasma membrane &
tonoplast
Na^+/H^+ antiporters

Chaves et al., 2002; Ashraf, 2010

Role of ABA in Drought Resistance



ABA mediates stomatal closing

ABA inhibits stomatal opening

Kwak et al., 2001

Major Signal Transduction Pathways under Abiotic Stress (Drought, Salt, Osmotic Stress)

- ABA (Dependant and) Signaling
- MAPK mediated Signaling
- *SOS* Signaling
- Phospholipid Signaling

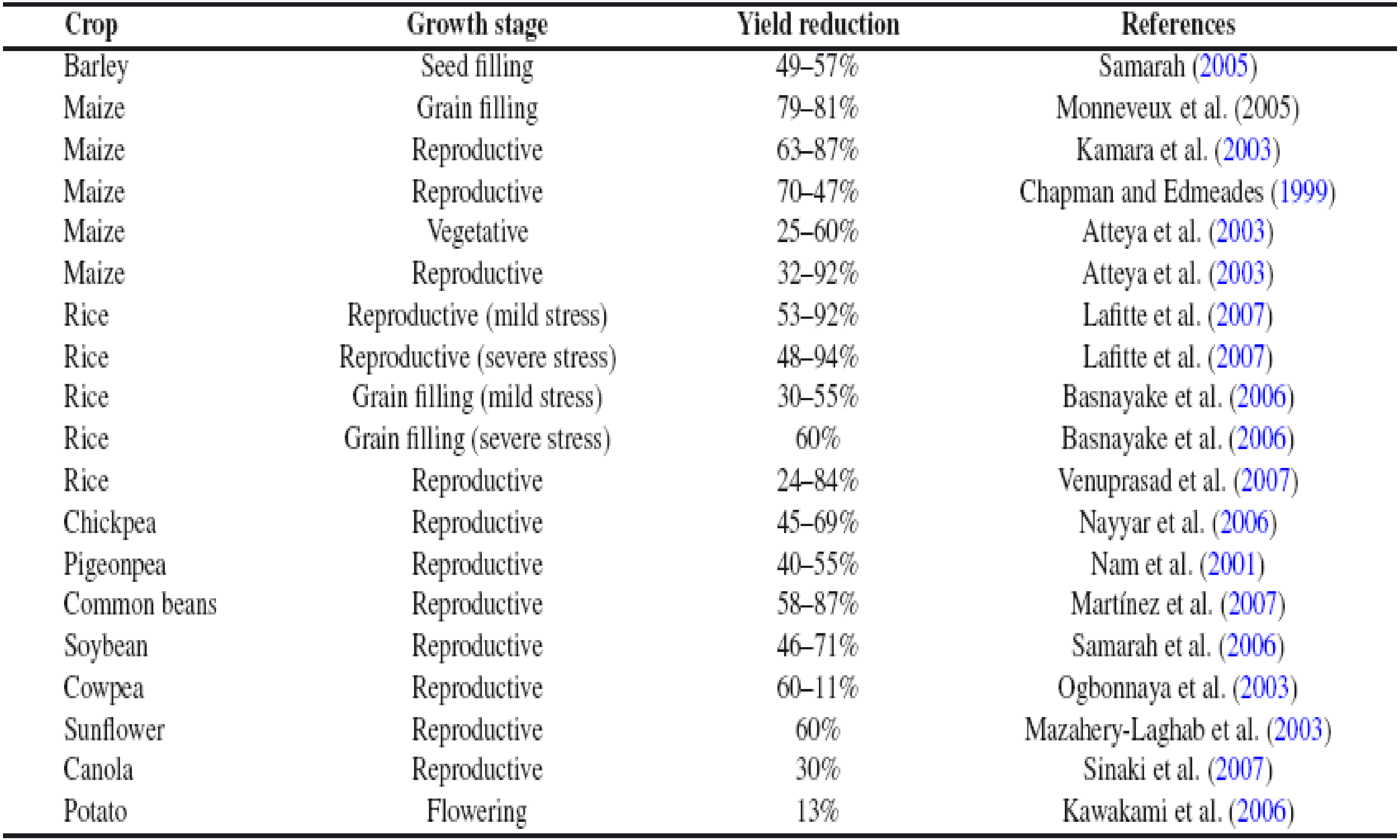
Physiological Indicators as Selection Criteria

Crop/Species	**Drought level**	**Physiological Attributes**	**Reference**
Wheat (*Triticum aestivum* L.)	At anthesis stage (Withholding water for 20 days from initiation of flower till start of grain formation)	Relative water content, stomatal conductance, leaf area and spike fertility were generally reliable indicators for screening drought tolerant wheat cultivars having potentially higher yields	Jatoi et al., 2011
Wheat (*Triticum aestivum* L.)	-1.2 MPa	Excised leaf water retention (ELWR) shows significant correlation with grain yield	Lonbani and Arzani, 2011
Chickpea (*Cicer arietinum*)	Only two irrigation under stress conditions as compared to six irrigations under non stress conditions	Well-defined relationships between drought susceptibility index and relative water content, chlorophyll and carotenoid concentration, Na and K uptake were found	Talebi et al., 2013
Wheat (*Triticum aestivum* L.)	withholding water for 6 days	High Stomatal Resistance (SR), Leaf Relative Water Content (LRWC), Vegetative Water Use Efficiency and Vegetative Evapotranspiration Efficiency could be used for drought tolerance	Shahram Mohammady, 2000

Physiological Indicators as Selection Criteria

Crop/Species	Drought level	Physiological Attributes	Reference
Maize (*Zea mays* L.)	After anthesis no irrigation	Membrane injury and water potential could be used as selection criteria	Grzesiak et al., 2013
Wheat (*Triticum aestivum* L.)	After anthesis no irrigation	relative water content (RWC), relative chlorophyll content	Farshadfar, 2012
Wheat (*Triticum aestivum* L.)	Non-stressed plots were irrigated three times after anthesis, while stressed plots received no water.	Excised leaf water rentention (ELWR), relative water loss (RWL), and cell membrane stability (CMS) could be used as selection criteria	Geravandi et al., 2011
Wheat (*Triticum aestivum* L.)	Withholding water before start of anthesis	Relative water content (RWC), and chlorophyll *a* fluorescence could be used as selection criteria	Živčák et al., 2008

Economic Yield Reduction by Drought Stress in Some Field Crops



Crop	Growth stage	Yield reduction	References
Barley	Seed filling	49–57%	Samarah (2005)
Maize	Grain filling	79–81%	Monneveux et al. (2005)
Maize	Reproductive	63–87%	Kamara et al. (2003)
Maize	Reproductive	70–47%	Chapman and Edmeades (1999)
Maize	Vegetative	25–60%	Atteya et al. (2003)
Maize	Reproductive	32–92%	Atteya et al. (2003)
Rice	Reproductive (mild stress)	53–92%	Lafitte et al. (2007)
Rice	Reproductive (severe stress)	48–94%	Lafitte et al. (2007)
Rice	Grain filling (mild stress)	30–55%	Basnayake et al. (2006)
Rice	Grain filling (severe stress)	60%	Basnayake et al. (2006)
Rice	Reproductive	24–84%	Venuprasad et al. (2007)
Chickpea	Reproductive	45–69%	Nayyar et al. (2006)
Pigeonpea	Reproductive	40–55%	Nam et al. (2001)
Common beans	Reproductive	58–87%	Martínez et al. (2007)
Soybean	Reproductive	46–71%	Samarah et al. (2006)
Cowpea	Reproductive	60–11%	Ogbonnaya et al. (2003)
Sunflower	Reproductive	60%	Mazahery-Laghab et al. (2003)
Canola	Reproductive	30%	Sinaki et al. (2007)
Potato	Flowering	13%	Kawakami et al. (2006)

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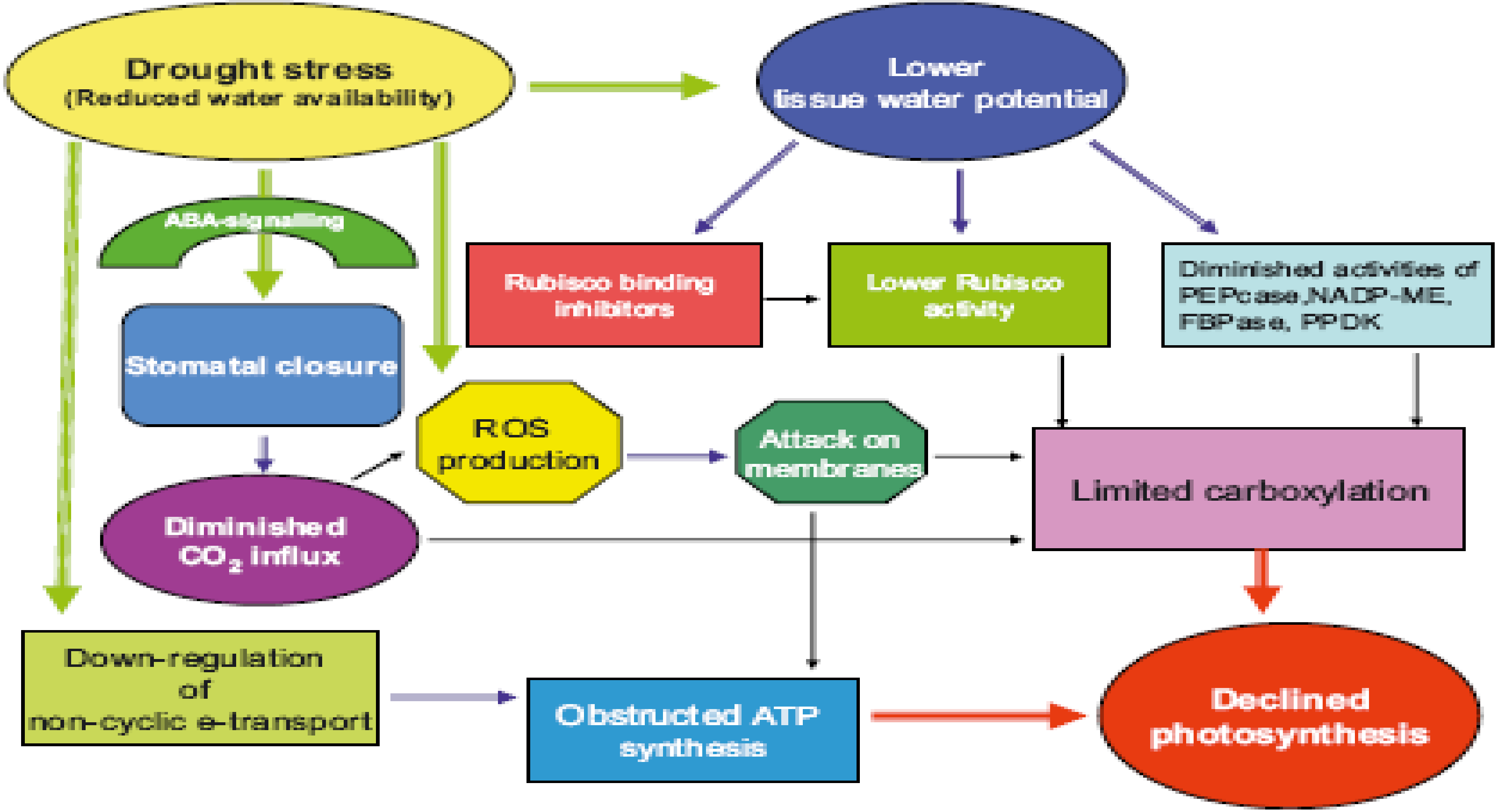
Effect of Drought on Photosynthesis



Drought stress
(Reduced water availability)

Lower
tissue water potential

ABA-signalling

Stomatal closure

Rubisco binding inhibitors

Lower Rubisco activity

Diminished activities of PEPcase,NADP-ME, FBPase, PPDK

ROS production

Attack on membranes

Limited carboxylation

Diminished CO_2 influx

Down-regulation of non-cyclic e-transport

Obstructed ATP synthesis

Declined photosynthesis

Farooq et al., 2009

Improving Drought Stress Tolerance

A Variety of Approaches:

1. Biotic approach is more useful to counteract drought-induced adverse effects
   - Screening and selection
   - Conventional Breeding
   - Shotgun approaches
     - ✓Seed priming
     - ✓Rooting medium
     - ✓Foliar spray
2. Molecular approaches
   - ✓Molecular marker assisted selection
   - ✓Transgenics

Biotic Approaches: Not so Simple! Complexicity due to:

- Drought stress tolerance is a quantitative trait
- Having complex phenotype
- Often confounded by plant phenology
- A number of abiotic stresses, such as high temperatures, high irradiance, and nutrient toxicities/deficiencies can challenge crop plants simultaneously

QTL Mapping

- Marker-assisted breeding (MAB) is a more efficient approach identifies thousands of genomic regions of a crop under stress conditions
- Comprehensive molecular linkage maps, marker-assisted selection procedures have led to pyramiding desirable traits to achieve improvements in crop drought tolerance

Problematic due to !!!

- Accuracy and preciseness in QTL identification
- Genetic × Environment interaction
- Large number of genes encoding yield
- Use of wrong mapping populations, have all harmed programs involved in mapping of QTL under limited conditions

Shotgun Approaches Exogenous Application of:

- Osmoprotectants
- Mineral Nutrients
- Plant Growth Regulators
- Antioxidants

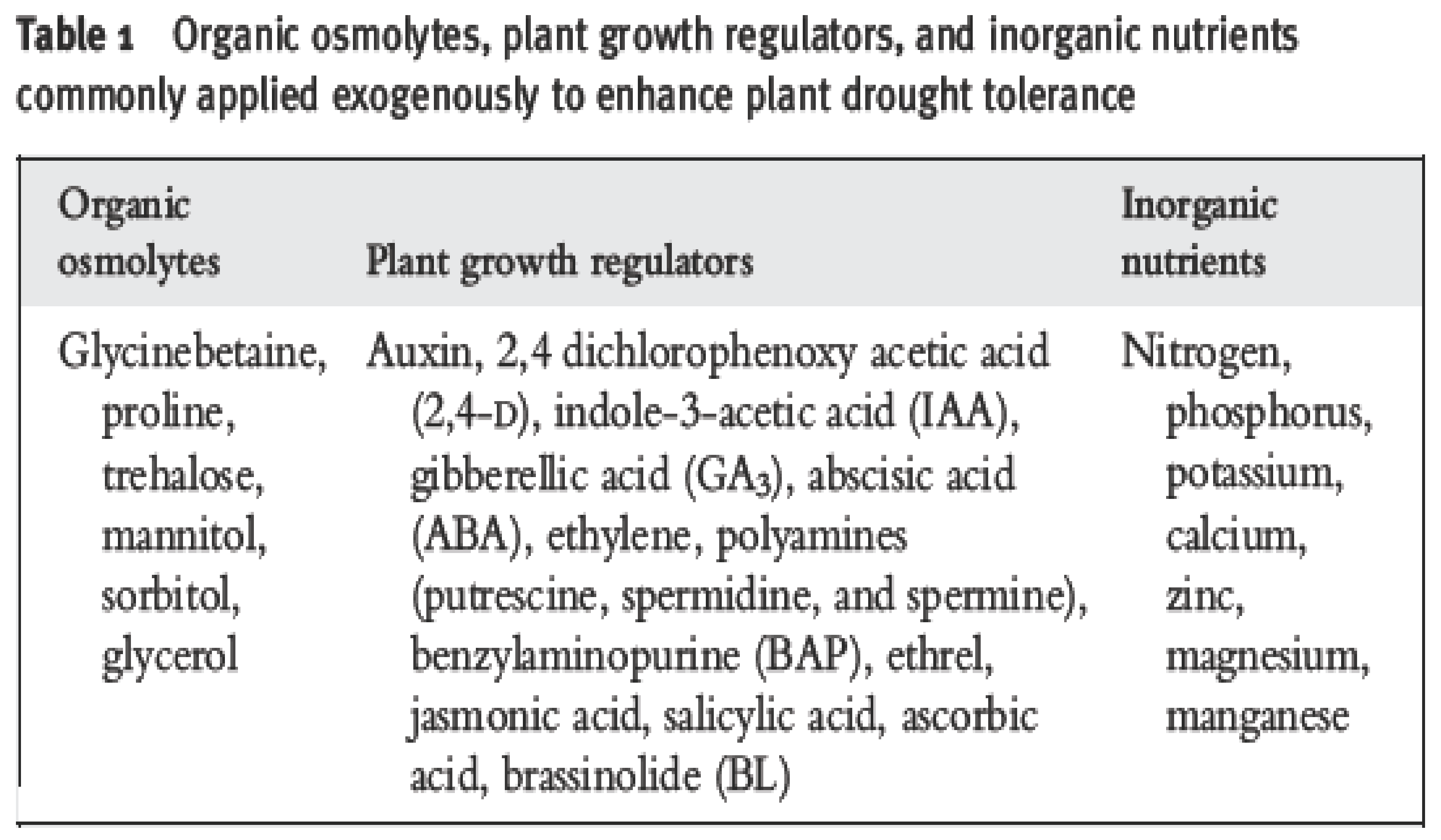
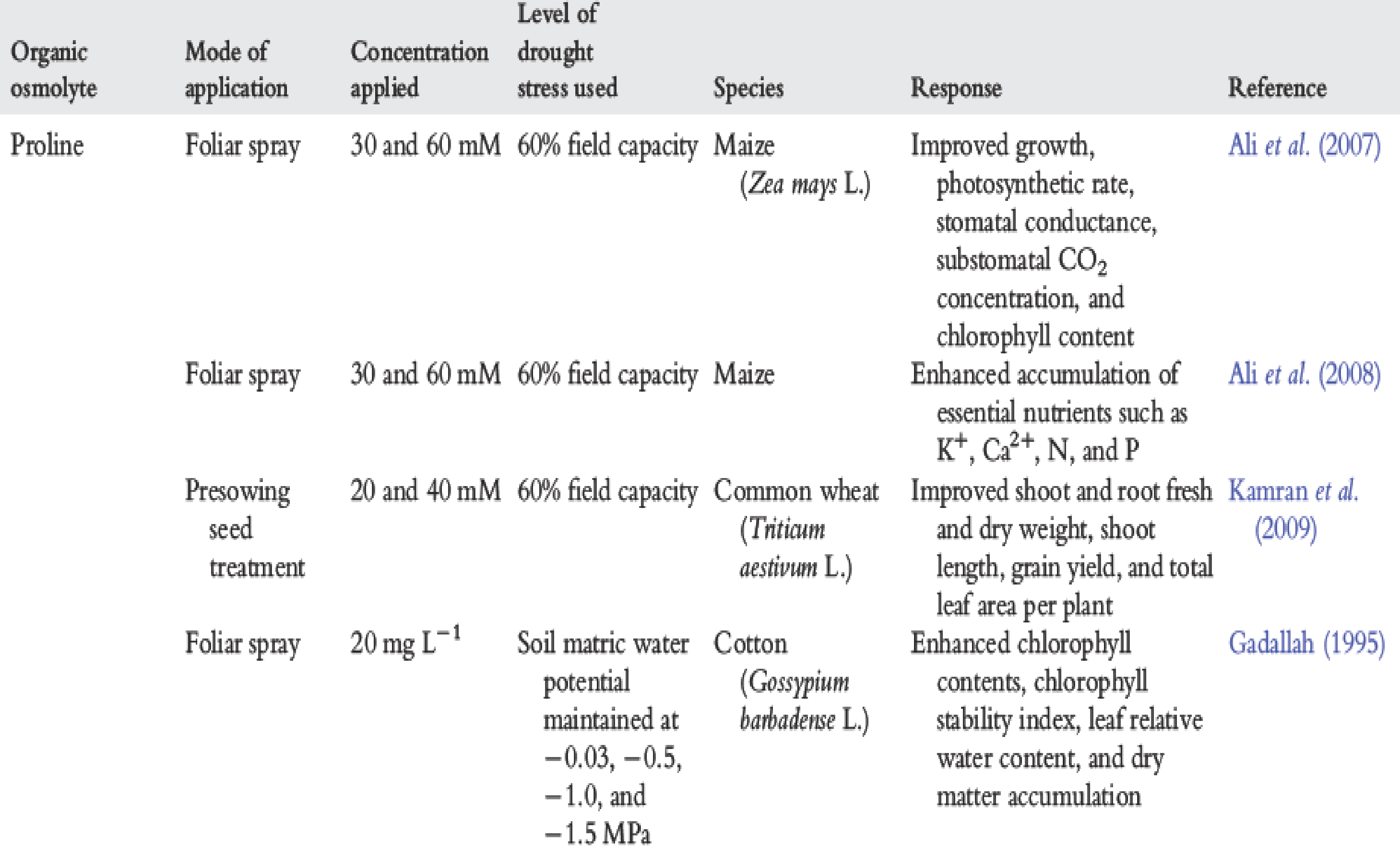


Table 1 Organic osmolytes, plant growth regulators, and inorganic nutrients commonly applied exogenously to enhance plant drought tolerance

Organic osmolytes	Plant growth regulators	Inorganic nutrients
Glycinebetaine, proline, trehalose, mannitol, sorbitol, glycerol	Auxin, 2,4 dichlorophenoxy acetic acid (2,4-D), indole-3-acetic acid (IAA), gibberellic acid (GA_3), abscisic acid (ABA), ethylene, polyamines (putrescine, spermidine, and spermine), benzylaminopurine (BAP), ethrel, jasmonic acid, salicylic acid, ascorbic acid, brassinolide (BL)	Nitrogen, phosphorus, potassium, calcium, zinc, magnesium, manganese

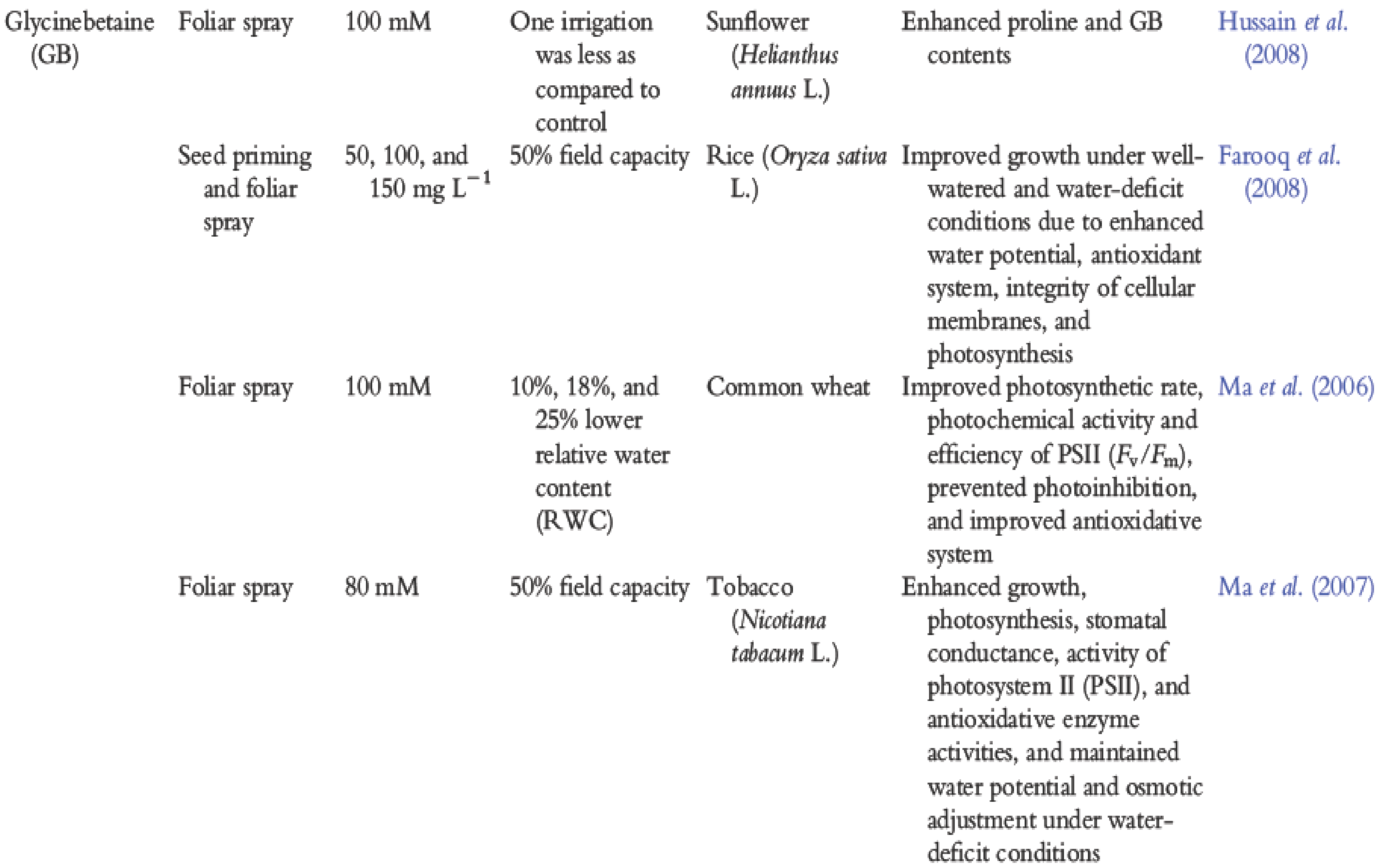
Antioxidants: **Ascorbic acid, α-tocopherol**

Exogenous Application of Organic Osmolytes



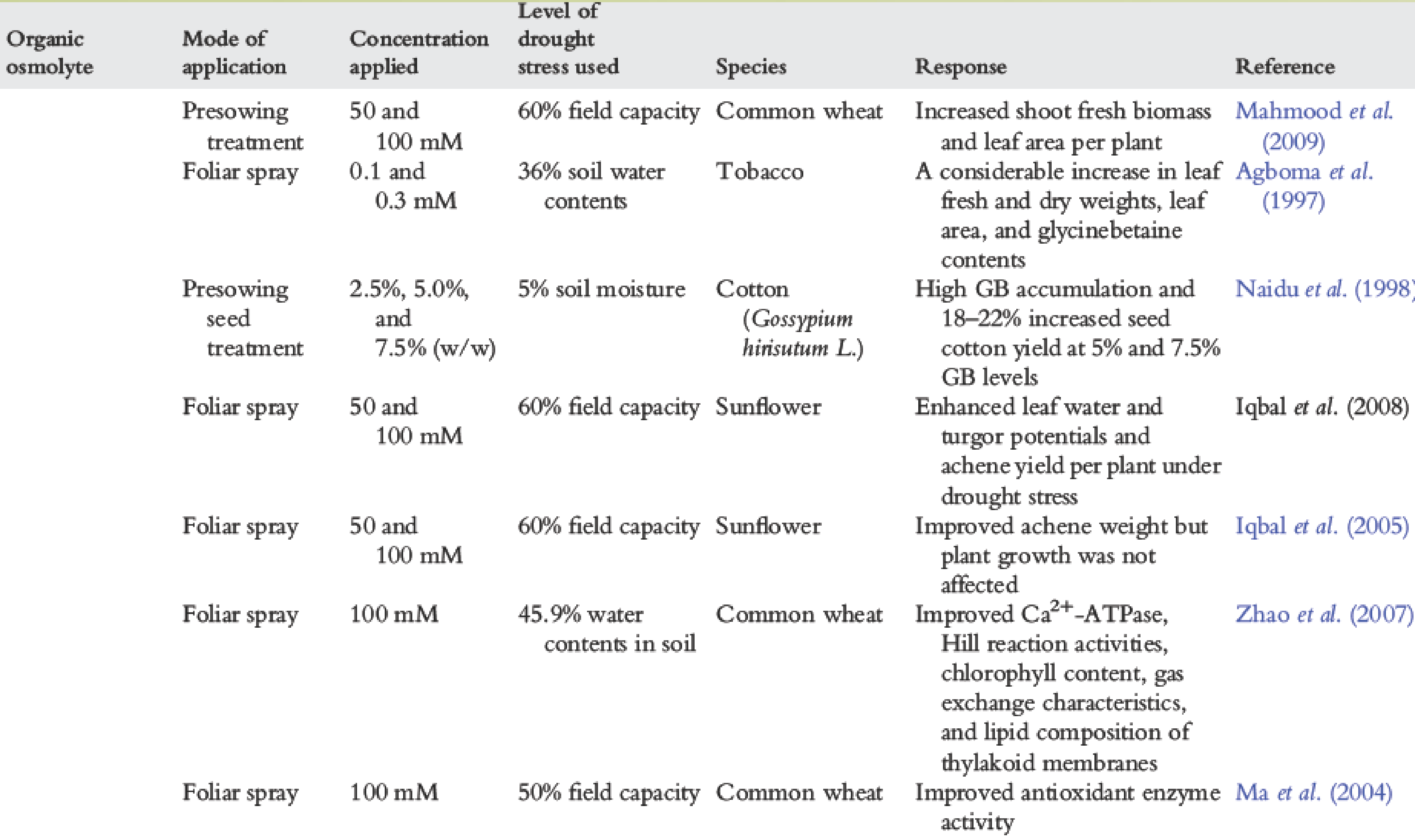
Organic osmolyte	Mode of application	Concentration applied	Level of drought stress used	Species	Response	Reference
Proline	Foliar spray	30 and 60 mM	60% field capacity	Maize (*Zea mays* L.)	Improved growth, photosynthetic rate, stomatal conductance, substomatal CO_2 concentration, and chlorophyll content	Ali *et al.* (2007)
	Foliar spray	30 and 60 mM	60% field capacity	Maize	Enhanced accumulation of essential nutrients such as K^+, Ca^{2+}, N, and P	Ali *et al.* (2008)
	Presowing seed treatment	20 and 40 mM	60% field capacity	Common wheat (*Triticum aestivum* L.)	Improved shoot and root fresh and dry weight, shoot length, grain yield, and total leaf area per plant	Kamran *et al.* (2009)
	Foliar spray	20 mg L^{-1}	Soil matric water potential maintained at −0.03, −0.5, −1.0, and −1.5 MPa	Cotton (*Gossypium barbadense* L.)	Enhanced chlorophyll contents, chlorophyll stability index, leaf relative water content, and dry matter accumulation	Gadallah (1995)

Exogenous Application of Organic Osmolytes



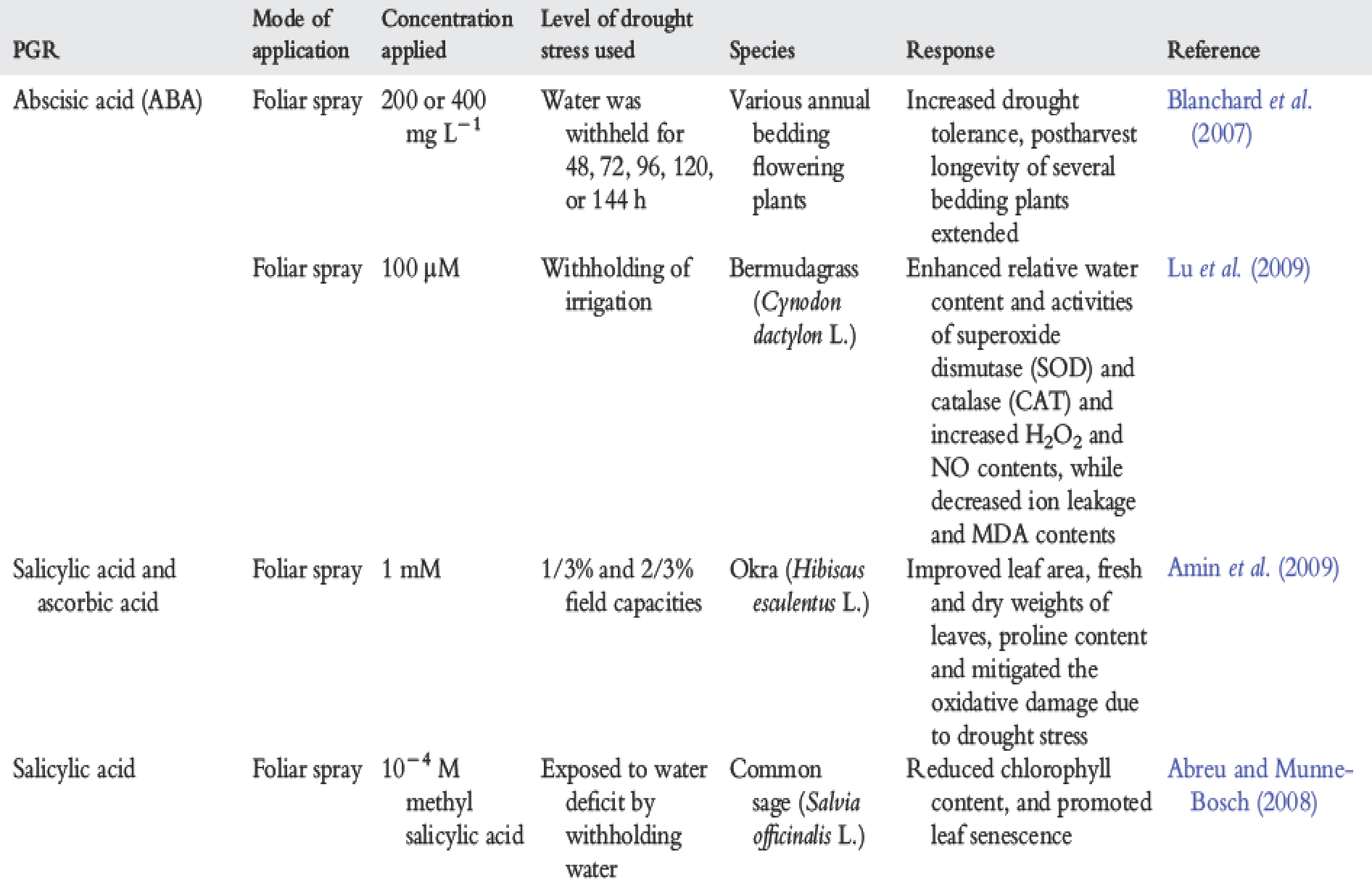
Glycinebetaine (GB)	Foliar spray	100 mM	One irrigation was less as compared to control	Sunflower (*Helianthus annuus* L.)	Enhanced proline and GB contents	Hussain *et al.* (2008)
	Seed priming and foliar spray	50, 100, and 150 mg L^{-1}	50% field capacity	Rice (*Oryza sativa* L.)	Improved growth under well-watered and water-deficit conditions due to enhanced water potential, antioxidant system, integrity of cellular membranes, and photosynthesis	Farooq *et al.* (2008)
	Foliar spray	100 mM	10%, 18%, and 25% lower relative water content (RWC)	Common wheat	Improved photosynthetic rate, photochemical activity and efficiency of PSII (F_v/F_m), prevented photoinhibition, and improved antioxidative system	Ma *et al.* (2006)
	Foliar spray	80 mM	50% field capacity	Tobacco (*Nicotiana tabacum* L.)	Enhanced growth, photosynthesis, stomatal conductance, activity of photosystem II (PSII), and antioxidative enzyme activities, and maintained water potential and osmotic adjustment under water-deficit conditions	Ma *et al.* (2007)

Exogenous Application of Organic Osmolytes



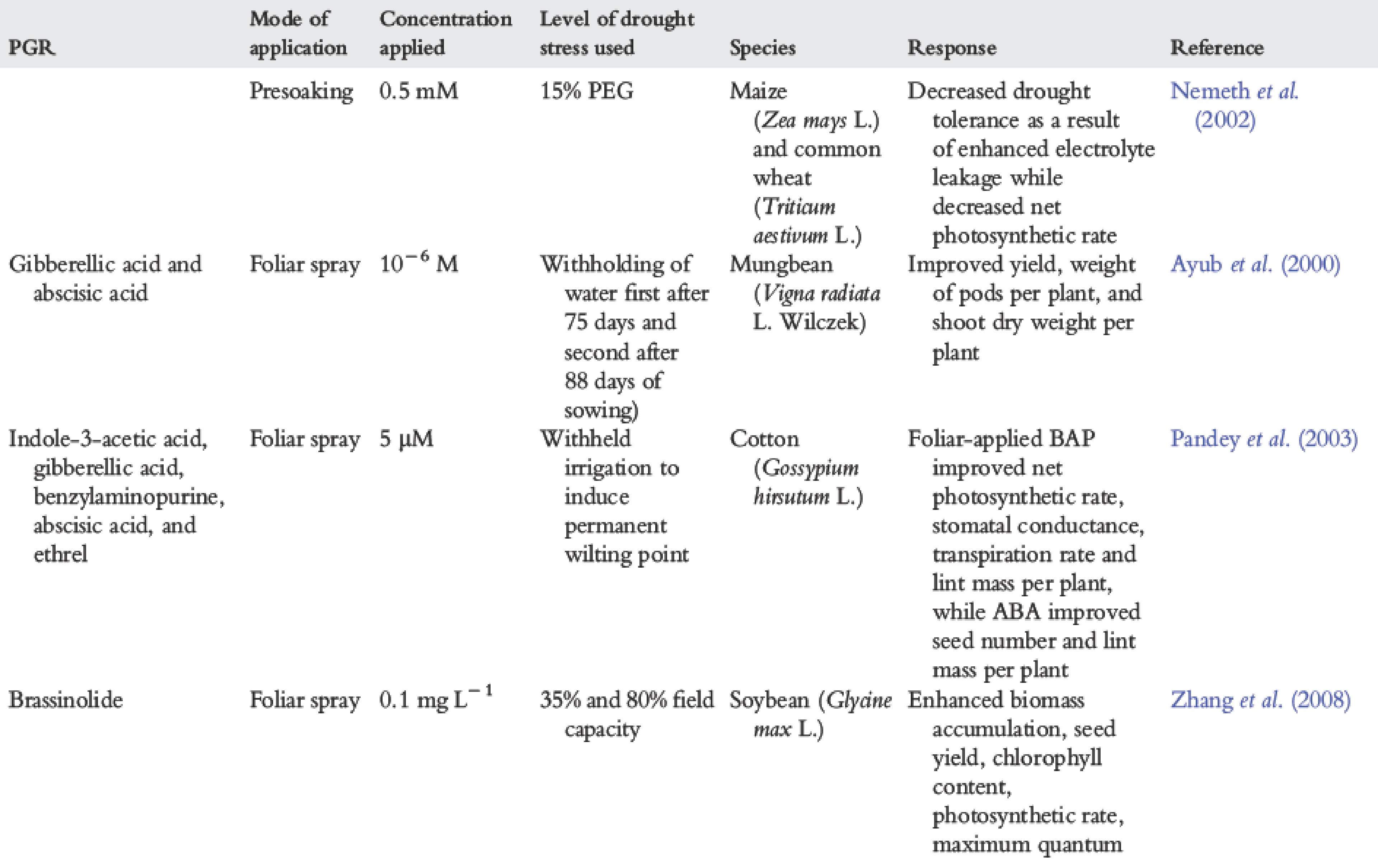
Organic osmolyte	Mode of application	Concentration applied	Level of drought stress used	Species	Response	Reference
	Presowing treatment	50 and 100 mM	60% field capacity	Common wheat	Increased shoot fresh biomass and leaf area per plant	Mahmood *et al.* (2009)
	Foliar spray	0.1 and 0.3 mM	36% soil water contents	Tobacco	A considerable increase in leaf fresh and dry weights, leaf area, and glycinebetaine contents	Agboma *et al.* (1997)
	Presowing seed treatment	2.5%, 5.0%, and 7.5% (w/w)	5% soil moisture	Cotton (*Gossypium hirisutum L.*)	High GB accumulation and 18–22% increased seed cotton yield at 5% and 7.5% GB levels	Naidu *et al.* (1998
	Foliar spray	50 and 100 mM	60% field capacity	Sunflower	Enhanced leaf water and turgor potentials and achene yield per plant under drought stress	Iqbal *et al.* (2008)
	Foliar spray	50 and 100 mM	60% field capacity	Sunflower	Improved achene weight but plant growth was not affected	Iqbal *et al.* (2005)
	Foliar spray	100 mM	45.9% water contents in soil	Common wheat	Improved Ca^{2+}-ATPase, Hill reaction activities, chlorophyll content, gas exchange characteristics, and lipid composition of thylakoid membranes	Zhao *et al.* (2007
	Foliar spray	100 mM	50% field capacity	Common wheat	Improved antioxidant enzyme activity	Ma *et al.* (2004)

Exogenous Application of Plant Growth Regulators



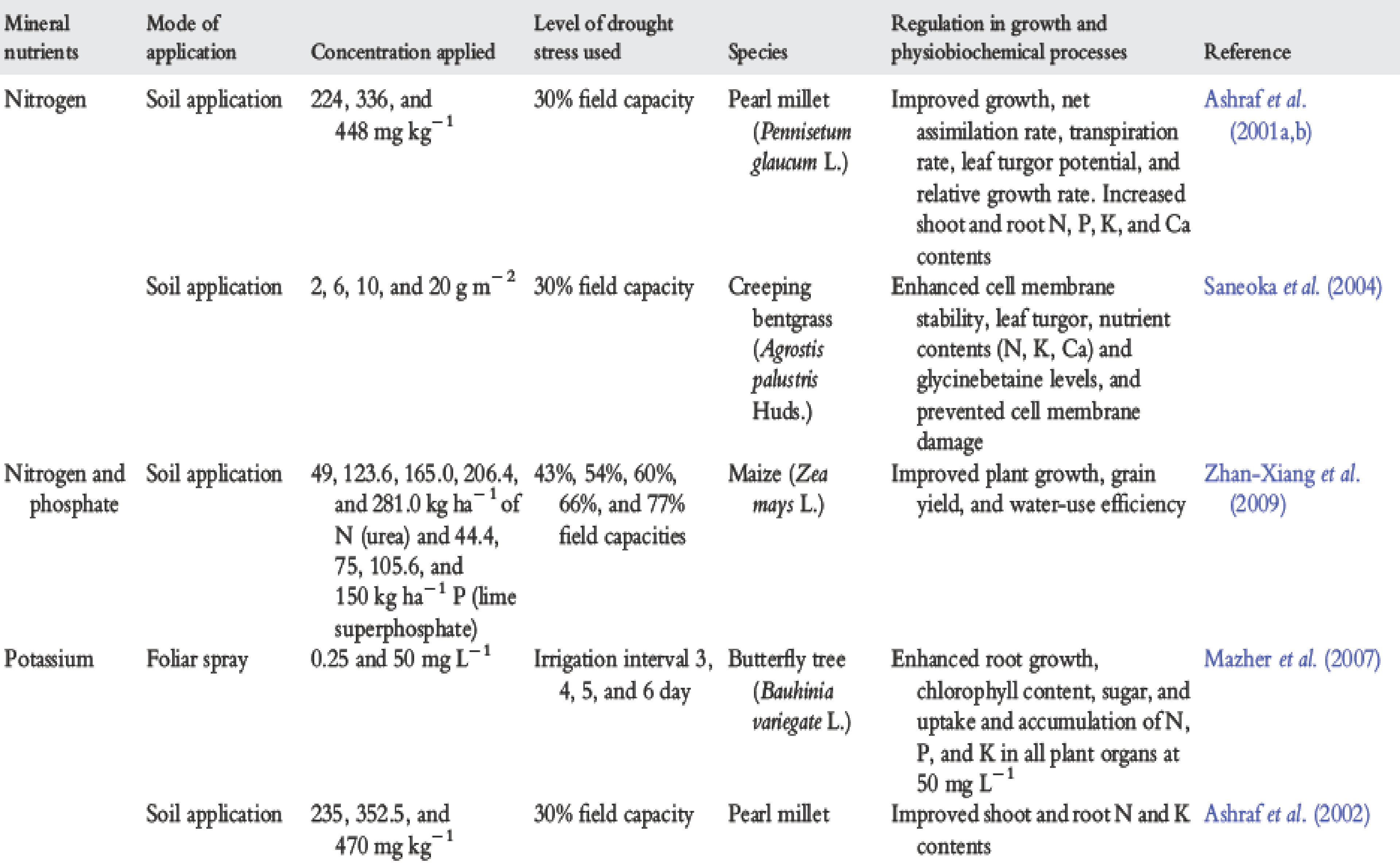
PGR	Mode of application	Concentration applied	Level of drought stress used	Species	Response	Reference
Abscisic acid (ABA)	Foliar spray	200 or 400 mg L^{-1}	Water was withheld for 48, 72, 96, 120, or 144 h	Various annual bedding flowering plants	Increased drought tolerance, postharvest longevity of several bedding plants extended	Blanchard *et al.* (2007)
	Foliar spray	100 µM	Withholding of irrigation	Bermudagrass (*Cynodon dactylon* L.)	Enhanced relative water content and activities of superoxide dismutase (SOD) and catalase (CAT) and increased H_2O_2 and NO contents, while decreased ion leakage and MDA contents	Lu *et al.* (2009)
Salicylic acid and ascorbic acid	Foliar spray	1 mM	1/3% and 2/3% field capacities	Okra (*Hibiscus esculentus* L.)	Improved leaf area, fresh and dry weights of leaves, proline content and mitigated the oxidative damage due to drought stress	Amin *et al.* (2009)
Salicylic acid	Foliar spray	10^{-4} M methyl salicylic acid	Exposed to water deficit by withholding water	Common sage (*Salvia officinalis* L.)	Reduced chlorophyll content, and promoted leaf senescence	Abreu and Munne-Bosch (2008)

Exogenous Application of Plant Growth Regulators



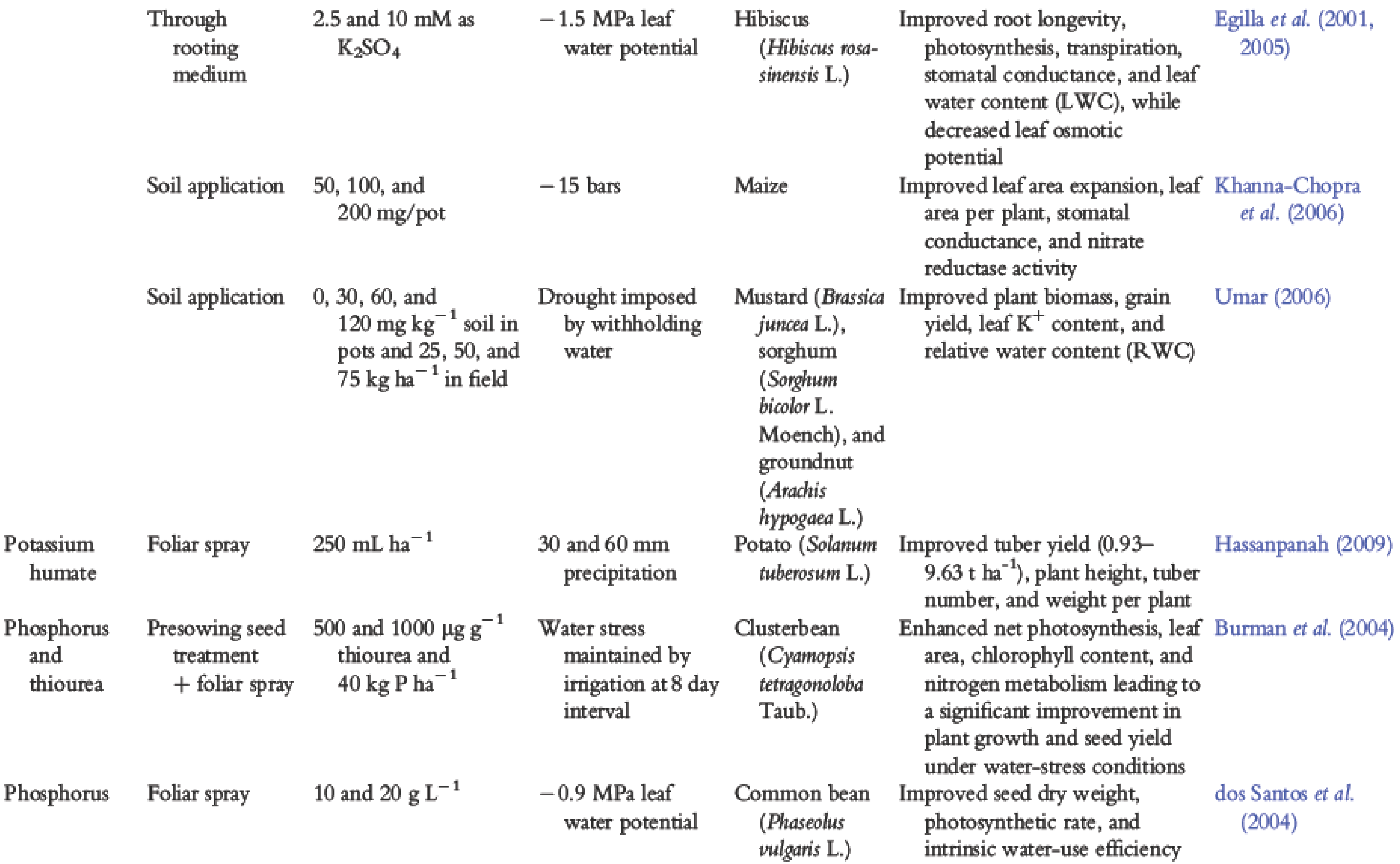
PGR	Mode of application	Concentration applied	Level of drought stress used	Species	Response	Reference
	Presoaking	0.5 mM	15% PEG	Maize (*Zea mays* L.) and common wheat (*Triticum aestivum* L.)	Decreased drought tolerance as a result of enhanced electrolyte leakage while decreased net photosynthetic rate	Nemeth *et al.* (2002)
Gibberellic acid and abscisic acid	Foliar spray	10^{-6} M	Withholding of water first after 75 days and second after 88 days of sowing)	Mungbean (*Vigna radiata* L. Wilczek)	Improved yield, weight of pods per plant, and shoot dry weight per plant	Ayub *et al.* (2000)
Indole-3-acetic acid, gibberellic acid, benzylaminopurine, abscisic acid, and ethrel	Foliar spray	5 µM	Withheld irrigation to induce permanent wilting point	Cotton (*Gossypium hirsutum* L.)	Foliar-applied BAP improved net photosynthetic rate, stomatal conductance, transpiration rate and lint mass per plant, while ABA improved seed number and lint mass per plant	Pandey *et al.* (2003)
Brassinolide	Foliar spray	0.1 mg L^{-1}	35% and 80% field capacity	Soybean (*Glycine max* L.)	Enhanced biomass accumulation, seed yield, chlorophyll content, photosynthetic rate, maximum quantum	Zhang *et al.* (2008)

Exogenous Application of Mineral Nutrients



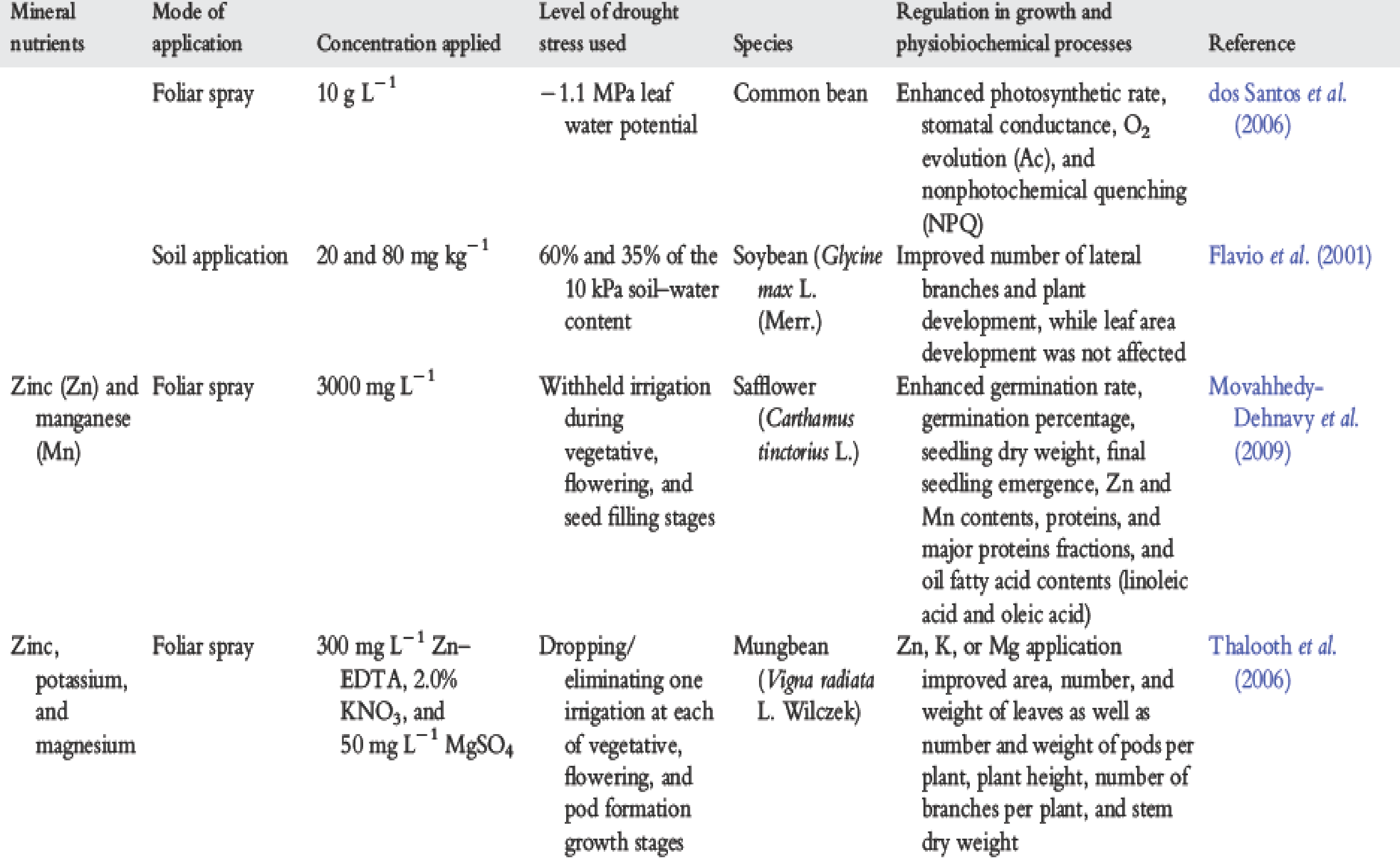
Mineral nutrients	Mode of application	Concentration applied	Level of drought stress used	Species	Regulation in growth and physiobiochemical processes	Reference
Nitrogen	Soil application	224, 336, and 448 mg kg^{-1}	30% field capacity	Pearl millet (*Pennisetum glaucum* L.)	Improved growth, net assimilation rate, transpiration rate, leaf turgor potential, and relative growth rate. Increased shoot and root N, P, K, and Ca contents	Ashraf *et al.* (2001a,b)
	Soil application	2, 6, 10, and 20 g m^{-2}	30% field capacity	Creeping bentgrass (*Agrostis palustris* Huds.)	Enhanced cell membrane stability, leaf turgor, nutrient contents (N, K, Ca) and glycinebetaine levels, and prevented cell membrane damage	Saneoka *et al.* (2004)
Nitrogen and phosphate	Soil application	49, 123.6, 165.0, 206.4, and 281.0 kg ha^{-1} of N (urea) and 44.4, 75, 105.6, and 150 kg ha^{-1} P (lime superphosphate)	43%, 54%, 60%, 66%, and 77% field capacities	Maize (*Zea mays* L.)	Improved plant growth, grain yield, and water-use efficiency	Zhan-Xiang *et al.* (2009)
Potassium	Foliar spray	0.25 and 50 mg L^{-1}	Irrigation interval 3, 4, 5, and 6 day	Butterfly tree (*Bauhinia variegate* L.)	Enhanced root growth, chlorophyll content, sugar, and uptake and accumulation of N, P, and K in all plant organs at 50 mg L^{-1}	Mazher *et al.* (2007)
	Soil application	235, 352.5, and 470 mg kg^{-1}	30% field capacity	Pearl millet	Improved shoot and root N and K contents	Ashraf *et al.* (2002)

Exogenous Application of Mineral Nutrients



	Through rooting medium	2.5 and 10 mM as K_2SO_4	−1.5 MPa leaf water potential	Hibiscus (*Hibiscus rosa-sinensis* L.)	Improved root longevity, photosynthesis, transpiration, stomatal conductance, and leaf water content (LWC), while decreased leaf osmotic potential	Egilla *et al.* (2001, 2005)
	Soil application	50, 100, and 200 mg/pot	−15 bars	Maize	Improved leaf area expansion, leaf area per plant, stomatal conductance, and nitrate reductase activity	Khanna-Chopra *et al.* (2006)
	Soil application	0, 30, 60, and 120 mg kg^{-1} soil in pots and 25, 50, and 75 kg ha^{-1} in field	Drought imposed by withholding water	Mustard (*Brassica juncea* L.), sorghum (*Sorghum bicolor* L. Moench), and groundnut (*Arachis hypogaea* L.)	Improved plant biomass, grain yield, leaf K^+ content, and relative water content (RWC)	Umar (2006)
Potassium humate	Foliar spray	250 mL ha^{-1}	30 and 60 mm precipitation	Potato (*Solanum tuberosum* L.)	Improved tuber yield (0.93–9.63 t ha^{-1}), plant height, tuber number, and weight per plant	Hassanpanah (2009)
Phosphorus and thiourea	Presowing seed treatment + foliar spray	500 and 1000 μg g^{-1} thiourea and 40 kg P ha^{-1}	Water stress maintained by irrigation at 8 day interval	Clusterbean (*Cyamopsis tetragonoloba* Taub.)	Enhanced net photosynthesis, leaf area, chlorophyll content, and nitrogen metabolism leading to a significant improvement in plant growth and seed yield under water-stress conditions	Burman *et al.* (2004)
Phosphorus	Foliar spray	10 and 20 g L^{-1}	−0.9 MPa leaf water potential	Common bean (*Phaseolus vulgaris* L.)	Improved seed dry weight, photosynthetic rate, and intrinsic water-use efficiency	dos Santos *et al.* (2004)

Exogenous Application of Mineral Nutrients



Mineral nutrients	Mode of application	Concentration applied	Level of drought stress used	Species	Regulation in growth and physiobiochemical processes	Reference
	Foliar spray	10 g L^{-1}	−1.1 MPa leaf water potential	Common bean	Enhanced photosynthetic rate, stomatal conductance, O_2 evolution (Ac), and nonphotochemical quenching (NPQ)	dos Santos *et al.* (2006)
	Soil application	20 and 80 mg kg^{-1}	60% and 35% of the 10 kPa soil–water content	Soybean (*Glycine max* L. (Merr.)	Improved number of lateral branches and plant development, while leaf area development was not affected	Flavio *et al.* (2001)
Zinc (Zn) and manganese (Mn)	Foliar spray	3000 mg L^{-1}	Withheld irrigation during vegetative, flowering, and seed filling stages	Safflower (*Carthamus tinctorius* L.)	Enhanced germination rate, germination percentage, seedling dry weight, final seedling emergence, Zn and Mn contents, proteins, and major proteins fractions, and oil fatty acid contents (linoleic acid and oleic acid)	Movahhedy-Dehnavy *et al.* (2009)
Zinc, potassium, and magnesium	Foliar spray	300 mg L^{-1} Zn–EDTA, 2.0% KNO_3, and 50 mg L^{-1} $MgSO_4$	Dropping/eliminating one irrigation at each of vegetative, flowering, and pod formation growth stages	Mungbean (*Vigna radiata* L. Wilczek)	Zn, K, or Mg application improved area, number, and weight of leaves as well as number and weight of pods per plant, plant height, number of branches per plant, and stem dry weight	Thalooth *et al.* (2006)

Drought tolerance in plants can be improved by engineering them to activate water-conserving processes in response to an agrochemical already in use

The transgenic (right) but not non-transgenic *Arabidopsis* plants (left) showed improved survival after withheld of water for 12 days, which cause severe wilting, and the plants are then re-watered to assess survival.

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Drought Tolerant Transgenic Plants
Very few reports: need to increase

Transgenic Crop/Species	Gene/Transcription factor	Physiological Attributes	Reference
Rice	*HOMEODOMAIN GLABROUS11* (*EDT1/HDG11*)	The transgenic rice plants also had higher levels of abscisic acid, proline, soluble sugar, and reactive oxygen species-scavenging enzyme activities during stress treatments	Yu et al., 2013
Rice	*Deeper Rooting 1* (*DRO1*)	Deeper roots, resulting in triple yields during drought	Uga et al., 2013
Wheat	DREB1A	Improved survival and recovery and water use efficiency under greenhouse conditions but not under field conditions	Pierre et al., 2012

Transgenic drought tolerant crops in commercial development and on the market

Developer	**Crop**	**Mechanism**	**Implementation location and status**	**Field trial results**
Monsanto	Corn	Expresses a cold-shock protein B from *B. subtilis*, which stabilizes RNA	Deregulated in US in December 2011; stewarded commercialization in US western Great Plains and Midwest	Average increase of five bushels of corn per acre during drought
PT Perkebunan Nusantara XI; University of Jember (East Java, Indonesia); Ajinomoto	Sugarcane	Expresses glycine betaine from *Rhizobium meliloti*	Approved in Indonesia by the National Genetically Modified Product Biosafety Commission in May 2013	20–30% higher sugar production than conventional counterparts during drought
Performance Plants (Kingston, Ontario)	Canola, corn, petunia and rice	Uses RNAi driven by conditional promoters to suppress farnesyltransferase; shuts down stomata	Licensed to Scotts (Marysville, Ohio), Syngenta (Basel), Bayer CropScience (Monheim, Germany), DuPont Pioneer, Mahyco (Jalna, India), RiceTec (Houston) and DBN (Beijing)	Canola, 26% higher yield; petunia, double the number of flowers
DuPont Pioneer	Corn	Expresses an ACS6 RNA construct to downregulate ACC synthase and decrease biosynthesis of ethylene	Field trials in the US and Chile	2.7-9.3 bushel per acre advantage over nontransgenic varieties in drought conditions

Nature Biotechnology 32, 610-613 (2014)

Transgenic drought tolerant crops in commercial development and on the market

Developer	**Crop**	**Mechanism**	**Implementation location and status**	**Field trial results**
Arcadia Biosciences	Rice and canola	Expresses isopentenyltransferase from Agrobacterium, which catalyzes the rate-limiting step in cytokinin synthesis; accompanied by SARK promoter from bean	Two years of US field trials in rice with combined WUE, NUE and salt tolerance; technology licensed to developers who have put the gene into their own varieties of soybean, wheat, rice, cotton, sugar beets, sugarcane and tree crops	13-18% under various nitrogen application rates; 12-17% under water stress conditions; 15% under combined stress
Verdeca, a joint venture of Arcadia Biosciences and Bioceres	Soybean	Overexpresses Hahb-4, from sunflower thought to inhibit ethylene-induced senescence	Field trials in Argentina and the US	7–15% yield advantage over comparable varieties during drought and other stress
Japan International Research Center for Agricultural Sciences	Wheat, soybean and sugarcane	Expresses DREB1A transcription factor under the control of the rd29A promoter	Field trials via collaborations with International Maize and Wheat Improvement Center, IRRI, International Center for Tropical Agriculture, Brazilian Enterprise for Agricultural Research	Varies

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Transgenic drought tolerant crops in commercial development and on the market

Developer	Crop	Mechanism	Implementation location and status	Field trial results
University of Tokyo and Japan International Research Center for Agricultural Sciences	Rice and peanut	Expresses DREB1A transcription factor under the control of the rd29A promoter	Field trials via collaborations with University of Calcutta (India, rice) and International Crops Research Institute for the Semi-Arid-Tropics (India, peanut)	Varies
Agricultural Genetic Engineering Research Institute (Giza, Egypt)	Wheat	Expresses HVA1 gene from barley, which confers osmotolerance	Conducting field trials and generating biosafety data required for approval by Egypt's regulatory authorities	Not disclosed
Indian Agricultural Research Institute (New Delhi)	Tomato	Overexpressing osmotin-encoding genes under the control of the 35S CMV promoter	Greenhouse studies in India	Better survival and growth: yield data not yet available

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Conclusions

- Organic osmolytes, PGRs, and mineral nutrients play essential roles in modulating plant growth and development under water stress.
- Plants can grow better in stressful environments either by increasing the intrinsic levels of these compounds through genetic modifications or by exogenous application of the corresponding compounds
- Currently, efforts are underway to develop more transgenic plants capable of producing higher levels of such compounds.
- Great attention has been devoted to enhancing plant performance under drought conditions by exogenous application of organic osmolytes, PGRs, or mineral nutrients via pre-sowing seed treatment, foliar application, or soil amendment.
- Rare testing of transgenic crops under field conditions

Future Prospects

Development of crop varieties with increased tolerance to drought, both by conventional breeding methods and by genetic engineering, is an important strategy to meet global food demands with less water

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My Research Group

**One Who Solves the Problem
of WATER is Worth Two
Noble Prizes:
One for Science
&
One for Piece
(John F. Kennedy)**