



Review

Induction of water stress in major *Solanum* crops: A review on methodologies and their application for identifying drought tolerant materials

Martín Flores-Saavedra, Mariola Plazas, Santiago Vilanova, Jaime Prohens, Pietro Gramazio*

Instituto de Conservación y Mejora de la Agrodiversidad Valenciana, Universitat Politècnica de València, Camino de Vera 14, 46022 Valencia, Spain

ARTICLE INFO

Keywords:

Solanum crops
Water stress
Stress tolerance
Stress induction methodologies
PEG
Wild species

ABSTRACT

The genus *Solanum* encompasses several economically important vegetable crops, such as tomato, potato, and eggplant, which are crucial for ensuring food security. Higher temperatures and reduced precipitation are becoming more frequent due to climate change in numerous regions, fostering drought spells and the likelihood of water stress in *Solanum* crops resulting in decreased yields. Appropriate evaluation techniques are required by researchers and breeders to evaluate the impact of drought on the performance of *Solanum* crops and identify more tolerant genotypes. This review examines the most important approaches for inducing water stress in *Solanum* crops, such as withholding irrigation, adjusting field capacity levels, applying evapotranspiration criteria, and utilizing polyethylene glycol as an osmotic agent. We highlight the benefits and drawbacks of each method, enabling researchers and breeders to choose the most suitable conditions for their specific objectives and goals. Additionally, we address the challenges of combining water stress with other types of stress that frequently occur simultaneously in the field and the effects that biostimulants can have in mitigating water stress in *Solanum* crops. We also provide an in-depth analysis of the impact of water deficit on growth and biomass, as well as on physiological and biochemical traits, and new phenotyping tools that allow the study of stress tolerance in the three major crops belonging to the *Solanum* genus. Finally, the review discusses the possibility of utilizing wild species to improve water stress tolerance in these *Solanum* crops.

1. Introduction

The Solanaceae family encompasses over 3000 species, with the genus *Solanum* comprising nearly half of these (Morris and Taylor, 2017). *Solanum* species are widely distributed worldwide with the greatest diversity found in the tropical regions of America, Australia, Africa and the Indo-Pacific (Echeverría-Londoño et al., 2020). Among them, three crops stand out for their agricultural and scientific importance: tomato (*S. lycopersicum* L.), potato (*S. tuberosum* L.), and eggplant (*S. melongena* L.). Tomato is the most important vegetable crop and a model species for fleshy-fruited plants (Schreinemachers et al., 2018), while potato is the most significant Solanaceae crop in total production and a key staple crop for food security and nutrition (Aksoy et al., 2021). Eggplant is the fifth most produced vegetable crop globally and a basic food product in many Asian countries (Oladosu et al., 2021).

Despite the dramatic increase in production and yield of these three *Solanum* crops in the last 50 years, a deceleration trend has been

observed with smaller yearly increases (FAO, 2020). Climate change is a major contributor to this trend, with higher temperatures and changes in precipitation patterns leading to harsher growth conditions and crop losses due to reduced water availability (Arnell et al., 2019; Cook et al., 2018). Higher evapotranspiration caused by higher temperatures, as well as salinity or drought, decreases the water available for plants, resulting in lower yield (Korres et al., 2016). Tomato and potato are highly sensitive to water deficit (Sakya et al., 2018; Hill et al., 2021), while eggplant can withstand low to moderate water deficiency, preserving its physiological processes and production under these conditions, but it is negatively affected by severe water shortage (Díaz-Pérez and Eaton, 2015). Technological improvements and solutions may mitigate the negative effects of drought in developed countries, but they may not be accessible in developing countries in the short run, where the effects are more severe and accelerated. Therefore, identifying more efficient and resilient genotypes is the most suitable, though challenging, solution (Solh and van Ginkel, 2014).

* Corresponding author.

E-mail address: piegra@upv.es (P. Gramazio).

<https://doi.org/10.1016/j.scienta.2023.112105>

Received 20 February 2023; Received in revised form 17 April 2023; Accepted 26 April 2023

Available online 3 May 2023

0304-4238/© 2023 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Table 1
Methods of induction of water stress in major *Solanum* cultivated species and wild relatives.

Methods of induction	Species	Stress level	Phenological stage during stress	Growing conditions	References	
Irrigation withholding	<i>S. lycopersicum</i>	Irrigation withholding for 7 days	Fruit development	Phytotron	Goel et al. (2010)	
		Irrigation withholding for 12 days	Leaf development	Growth chamber	Wu et al. (2017)	
		Irrigation withholding for 9 days	Leaf development	Growth chamber	Bian et al. (2019)	
		Irrigation withholding for 6 days	–	Growth chamber	Filiz and Akbudak (2020)	
		Irrigation withholding for 14 days	Leaf development	Greenhouse	Choi et al. (2011)	
		Irrigation withholding for 21 days	Leaf development	Greenhouse	Zhu et al. (2014)	
		Irrigation withholding for 16 days	Flowering	Greenhouse	Landi et al. (2016)	
		Irrigation withholding for 14 days	–	Greenhouse	Mishra et al. (2016)	
		Irrigation withholding for 19 days	Leaf development	Greenhouse	Tamburino et al. (2017)	
		Irrigation withholding for 14 days	–	Greenhouse	Karkute et al. (2018)	
		Irrigation withholding for 30 days	Fruit development	Greenhouse	Waseem et al. (2019)	
		Irrigation withholding for 10 days	Leaf development	Greenhouse	Akbudak et al. (2020)	
		Irrigation withholding for 45 days	Fruit development	Field	Landi et al. (2016)	
	<i>S. pennellii</i>	Irrigation withholding for 8 days	Leaf development (flowering)	Growth chamber	Egea et al. (2018)	
	<i>S. tuberosum</i>	Irrigation withholding for 14 days	Tuber formation	Greenhouse with natural light	Boguszewska et al. (2010)	
		Irrigation withholding for the remainder of the growing season	Leaf development	Field	Liu et al. (2020)	
	<i>S. melongena</i>	Irrigation withholding for 41 days	Tuber formation	Field	Schafleitner et al. (2007)	
		Irrigation withholding for 11 days	Leaf development	Greenhouse	Plazas et al. (2019)	
	<i>S. aethiopicum</i>	Irrigation withholding for 14 days	–	Field	Delfin et al. (2021)	
		Until showing symptoms of wilting	Leaf development	Greenhouse	Mibei et al. (2017)	
	Several eggplant CWR	<i>S. lycopersicum</i>	Irrigation withholding for 14 days	Leaf development	Greenhouse	Sseremba et al. (2018)
			Irrigation withholding for 11 days	Leaf development	Greenhouse	Plazas et al. (2022)
	Field Capacity	<i>S. lycopersicum</i>	Gradually increase of stress (75, 50 and 25% of FC)	–	Growth chamber	Hosseini Tafreshi et al. (2021)
60% of FC			Fruit development	Greenhouse	Rady et al. (2020)	
40, 25 and 15% of FC			–	Greenhouse	Krishna et al. (2021)	
<i>S. tuberosum</i>		50% of FC	Fruit development	Greenhouse	Azizi et al. (2021)	
		75% and 50% of FC	Flowering	Greenhouse with natural light	Chakma et al. (2021)	
		40–30% of FC	Tuber formation	Growth chamber	Gong et al. (2015)	
Field Capacity	<i>S. tuberosum</i>	25% of FC	Tuber initiation	Greenhouse and growth chamber	Szalonek et al. (2015)	
		50% of FC	Tuber initiation	Greenhouse	Rolando et al. (2015)	
		50 and 30% of FC	Tuber initiation	Shade-house	Ibañez et al. (2021)	
	<i>S. melongena</i>	30% of FC	Leaf development	Greenhouse	Fu et al. (2013)	
		25% of FC	Leaf development	Greenhouse	Tani et al. (2018)	
		Gradually increase stress (30 and 10% of FC)	–	Greenhouse	Delfin et al. (2021)	
Volumetric water content Evapotranspiration	<i>S. chilense</i>	75 and 50% of FC	Throughout the crop cycle	Field	Çolak et al. (2015)	
		20% of volumetric water content	–	Growth chamber	Blanchard-Gros et al. (2021)	
	<i>S. lycopersicum</i>	20% of ET ₀	–	Field	Galmés et al. (2013)	
		75 and 50% of ETc	Fruit development	Field	Takács et al. (2020)	
	<i>S. pimpinellifolium</i> and <i>S. lycopersicum</i> var. <i>cerasiforme</i>	60% of ETc	From flowering	Greenhouse	Albert et al. (2016)	
		40% of ETc	Throughout the crop cycle	Greenhouse	Martínez-Cuenca et al. (2020)	
	<i>S. tuberosum</i> <i>S. melongena</i>	60 and 40% of ET	Throughout the crop cycle	Field	della Costa et al. (1997)	
		67 y 33% de ETc	–	Field	Díaz-Pérez and Eaton (2015)	
		70 y 40% de ETc	Throughout the crop cycle	Field	Amiri Rodan et al. (2020)	
		60% de ETc	Throughout the crop cycle	Field	Semida et al. (2021)	
Polyethylene glycol	<i>S. lycopersicum</i>	10% PEG for 7 days	–	Growth chamber	Karaca and Cekic (2019)	
		20% PEG for 5 days	Leaf development	Incubation chamber	Meng et al. (2020)	
		15% PEG for 48 h	Leaf development	Hydroponic	Landi et al. (2016)	
		14 and 4% PEG	Germination	Seed germination	Esan et al. (2018)	
		6, 4 and 2% PEG	Leaf development	<i>In vitro</i>	Kulkarni and Deshpande (2010)	

(continued on next page)

Table 1 (continued)

Methods of induction	Species	Stress level	Phenological stage during stress	Growing conditions	References
	<i>S. tuberosum</i>	15% PEG for 6 h 25% PEG for 24 h 8 and 4% PEG	- Leaf development Leaf development	<i>In vitro</i> <i>In vitro</i> <i>In vitro</i>	Hwang et al. (2011) Kappachery et al. (2013) Pino et al. (2013)
	<i>S. melongena</i>	10% PEG for 24 h 10% PEG for 21 days 10, 8 and 3% of PEG for 21 days	Leaf development Leaf development Leaf development	<i>In vitro</i> <i>In vitro</i> <i>In vitro</i>	Liu et al. (2020) Siaga et al. (2016) Zayova et al. (2017)

Fortunately, within the gene pool of these three *Solanum* crops, genotypes adapted to water deficit have been identified, such as local varieties of tomato (Galmés et al., 2013) or wild relatives of potato (Ibañez et al., 2021) and eggplant (Plazas et al., 2022). In this regard, appropriate phenotyping is essential to identify genotypes adapted to drought conditions and high temperatures (Reynolds et al., 2020). However, due to the quantitative nature of the traits related to water deficit and the duration and intensity of water stresses, which are highly variable among the plant phenological stages, environments and crops, no consensus and universal protocols have been developed for comprehensive phenotype candidate genotypes (Passioura, 2012).

This paper aims at reviewing the state of the art of procedures and approaches to evaluate water stress in the three most important *Solanum* crops, comparing the water deficit induction methods according to different criteria and experimental conditions to identify the best stress-tolerant genotypes, providing relevant information and guidelines for developing suitable water stress phenotyping toolkits. The effects of drought combined with other stresses and the effects of biostimulants application are also being investigated, as well as the potential of wild relatives for improving the drought tolerance of the target crops is also reviewed.

2. Water deficit induction methods in *Solanum* crops

The methods to induce water deficit and evaluate growth parameters to test water stress tolerance in *Solanum* materials are very diverse. In greenhouse conditions, water deficit is often induced by withholding irrigation, simulating severe stress (Plazas et al., 2019; Akbudak et al., 2020) or by reducing irrigation to a certain percentage of field capacity (Tani et al., 2018; Azizi et al., 2021). In field conditions, water stress is typically induced by withholding irrigation (Landi et al., 2016) or by reducing evapotranspiration percentage (Galmés et al., 2013; Semida et al., 2021). On the other hand, when stress is evaluated *in vitro* or in climatic chambers, different concentrations of osmotic agents, such as polyethylene glycol, are added (Siaga et al., 2016; Liu et al., 2020).

2.1. Withholding irrigation

Withholding the irrigation supply is the simplest and easiest method to evaluate water stress tolerance, even though the developmental stage at which the withholding is applied and its duration are very variable (Table 1). In tomato, withholding of stress can be highly variable, being applied to underdeveloped plants 10 days after transplant (Tamburino et al., 2017) or more developed, after two months of growth (Filiz and Akbudak, 2020; Landi et al., 2016). Thus, the phenological stage where the water stress was applied, in most cases, is in the vegetative phase. However, it has also been evaluated in flowering or during fruit development (Table 1), so the effect of stress could be very different in each trial. In the case of potato and eggplant, less information is available regarding this method of stress induction. In potato, different authors have induced stress at different times of growth, either in leaf development (Liu et al., 2020) or tuber formation (Schafleitner et al., 2007; Boguszewska et al., 2010). In eggplant, stress was applied at the phenological stage of five true leaves in greenhouse trials (Plazas et al., 2019) or five weeks after transplantation in field trials (Delfin et al., 2021), while in the related scarlet eggplant (*S. aethiopicum* L.), the application of stress was performed five days after transplanting (Mibe et al., 2017) or after eight weeks in cultivation (Sseremba et al., 2018). Withholding the water supply at any phenological stage generates biomass and yield losses; however, the effects may be different at each stage (Yavuz et al., 2021).

The duration of stress also varies depending on the growing conditions, the plant material, and the level of stress applied. In tomato trials, for example, stress has been applied for periods ranging from 6 to 45 days (Table 1). In the cases mentioned, the time of exposure to stress did not have a direct relationship with the developmental stage of the crop.

In the case of *S. pennellii*, a wild relative of the tomato, stress was generated by withholding the water supply for eight days, being less affected than cultivated tomato (Egea et al., 2018). In potato, irrigation withholding was evaluated for 14 days (Boguszewska et al., 2010), 41 days (Schafleitner et al., 2007) or until the end of the growing season (Liu et al., 2020). On the other hand, irrigation withholding was assessed in eggplant for 11 days (Plazas et al., 2019) and 14 days (Delfin et al., 2021), while in scarlet eggplant it was applied for 14 days (Sseremba et al., 2018). The evapotranspiration demand of a crop can vary spatially and temporally (Christou et al., 2017), so a long time without irrigation does not necessarily imply a higher level of stress for the crop.

2.2. Watering to different field capacity levels

Soil field capacity (FC), a concept first introduced by Veihmeyer and Hendrickson (1931), and further developed over time (Zacharias and Bohne, 2008; Robertson et al., 2021), refers to the water content of soil or plant substrate after it has been saturated with water and then drained until the water drainage is no longer significant. Unlike the method of withholding water supply, this approach ensures that a certain level of water is available for the plant. The timing of stress application in tomato was done in plants aged from around 30 d (Azizi et al., 2021; Hosseini Tafreshi et al., 2021) to 50 d (Rady et al., 2020; Krishna et al., 2021). For potato plant, in most cases, induced stress in plants was performed in the phenological stage of the beginning of tuber formation (Rolando et al., 2015; Szalonek et al., 2015; Ibañez et al., 2021), while Gong et al. (2015) did it in the flowering stage (tuber formation). In the case of eggplant, water stress was applied during the leaf development stage, when plants had around five expanded leaves (Fu et al., 2013; Tani et al., 2018) or five weeks after transplanting (Delfin et al., 2021).

The percentage of FC used to induce water stress in plants varies depending on the objective of the study. In tomato plants, levels of FC up to 15% (Krishna et al., 2021) and 25% (Hosseini Tafreshi et al., 2021) were used to induce severe stress, while moderate stress was induced with FC levels of 50% (Azizi et al., 2021), 60% (Rady et al., 2020) or 75% (Chakma et al., 2021). In potato plants, severe stress was induced with FC levels of 25% (Szalonek et al., 2015), 30% (Ibañez et al., 2021) and 35% (Gong et al., 2015), while moderate stress was induced with FC levels of 50% (Ibañez et al., 2021; Rolando et al., 2015). For eggplant, more restrictive levels of irrigation were used, with FC levels of 10% (Delfin et al., 2021), 25% (Tani et al., 2018) and 30% (Fu et al., 2013) for severe stress, and less restrictive levels of 50% and 75% under field conditions (Çolak et al., 2015). Generally, to induce severe stress in these major Solanaceae crops, the values of FC range from 10 to 35%, while moderate stress ranges from 40 to 75% (Table 1). However, the level of stress also depends on the duration of exposure.

2.3. Evapotranspiration-based criteria

The combination of water loss through soil surface evaporation and crop transpiration is known as evapotranspiration (ET). This concept includes different definitions: reference evapotranspiration (ET_0), which is a parameter related to the evaporative power of a specific atmospheric environment, with a reference surface and without water restrictions (well-watered grass), while crop evapotranspiration (ETc) refers to the evapotranspiration of a specific crop, under optimal conditions, in a specific atmospheric environment (Pereira et al., 2015).

Evapotranspiration-based criteria have also been used to generate water stress in crops of the *Solanum* genus by decreasing the replenishment of the crop's total evapotranspiration. This method is mainly used in field trials. In tomato trials, water stress was induced after a month of well-irrigated cultivation by applying only 20% of the ET_0 (Galmés et al., 2013). A reduction in irrigation to 40% of the ETc at the beginning of flowering resulted in reductions in tomato vigor and yield

(Albert et al., 2016). Similarly, Martínez-Cuenca et al. (2020) evaluated *S. pimpinellifolium* and *S. lycopersicum* var. *cerasiforme* under the same stress level, resulting in negative effects on production. When less restrictive levels were applied, by irrigating tomato plants to 75% and 50% of the ETc until reaching the stage of the beginning of fruit ripening, Takács et al. (2020) found that plants irrigated to 75% ETc were not greatly affected, although significant yield reductions were observed in plants irrigated with 50% ETc. In potato, moderate stresses were achieved by irrigating to 60% ETc and severe stresses by irrigating to 40% ETc (dalla Costa, 1997). To induce water stress in eggplant, plants were exposed after four weeks of transplanting to 33% and 67% ETc (Díaz-Pérez and Eaton, 2015), 40% and 70% ETc when the plants had five to six true leaves (Amiri Rodan et al., 2020), and 60% ETc to 37-day-old plants (Semida et al., 2021).

Determining the ET requirements of a crop under water stress is complex, and the use of a percentage of the ETc often results in excessive or insufficient irrigation, depending on whether the ET_0 is high or low (Hochberg et al., 2017). Therefore, although it is a practical method under field conditions, the percentage used in one environment can have a different effect on the crop when evaluated in another environment.

2.4. Use of polyethylene glycol solutions

The use of polyethylene glycol (PEG) solutions as an osmotic agent results in a decrease in water potential (Al-Taisan et al., 2010), making it a useful tool for simulating water stress in studies of drought tolerance. In the case of *Solanum*, PEG has been used in hydroponic studies and *in vitro* culture (Table 1).

In tomato cultivation, germination tests were conducted using PEG concentrations of 0%, 4%, and 14% in distilled water, where higher concentrations reduced the percentages of germination and seedling growth (Esan et al., 2018). Under hydroponic conditions, tomato plants were subjected to a 15% PEG solution for 48 h, causing severe chlorosis and leaf loss (Landi et al., 2016). Similarly, tomato plants grown on perlite were watered with Hoagland solution with 10% PEG for four weeks (Karaca and Cekic, 2019). For *in vitro* evaluation, tomato seedlings were evaluated in Murashige and Skoog (MS) medium with 2%, 4% and 6% PEG concentrations, with growth decreasing as PEG concentration increased (Kulkarni and Deshpande, 2010). Notably, genotypes that were most tolerant in the *in vitro* assay also tended to be more tolerant under field conditions, suggesting that this method may have potential as a preliminary screening tool.

In potato, PEG tests were mainly conducted under *in vitro* culture conditions, using variable PEG concentrations to replace MS medium. Kappachery et al. (2013), grew plants for 28 days before applying 25% PEG, resulting in clear signs of wilting within 24 h. Pino et al. (2013) evaluated osmotic stress by performing *in vitro* culture tests with concentrations of 4% and 8% PEG, resulting in water potential values of -0.362 and -0.478 MPa, respectively. Liu et al. (2020) subjected potato seedlings to 10% PEG for 24 h to analyze gene expression under water stress.

In eggplant, Siaga et al. (2016), evaluated the growth of seedlings cultivated *in vitro* with 10% PEG for 21 days, which negatively impacted survival and growth, while Zayova et al. (2017) cultivated eggplant seedlings on 3%, 8% and 10% PEG for 21 days for stress induction, observing that higher PEG concentration resulted in lower survival rates.

This method allows for greater control over the level of stress generated compared to others, but it is not a practical method for evaluating crop biomass and yield, so results may not always apply to field conditions. While relationships have been reported between *in vitro* culture with PEG and open field culture for drought tolerance (Kulkarni and Deshpande, 2010; Gopal and Iwama, 2007), further trials are needed to validate the method.

Table 2

Comparison of stress induction methods in major *Solanum* crops. The number of asterisks indicates a higher relationship with the corresponding characteristic.

Characteristic	Irrigation withholding	Field capacity level	Evapotranspiration level	Polyethylene glycol
Area used	***/**	***/**	***/**	*
Control and replicability	*	**	**	***
Duration of the trial	***/**	***/**	***	*
Relationship with real conditions	***	***/**	***	*
Easy implementation	***	*	*	**

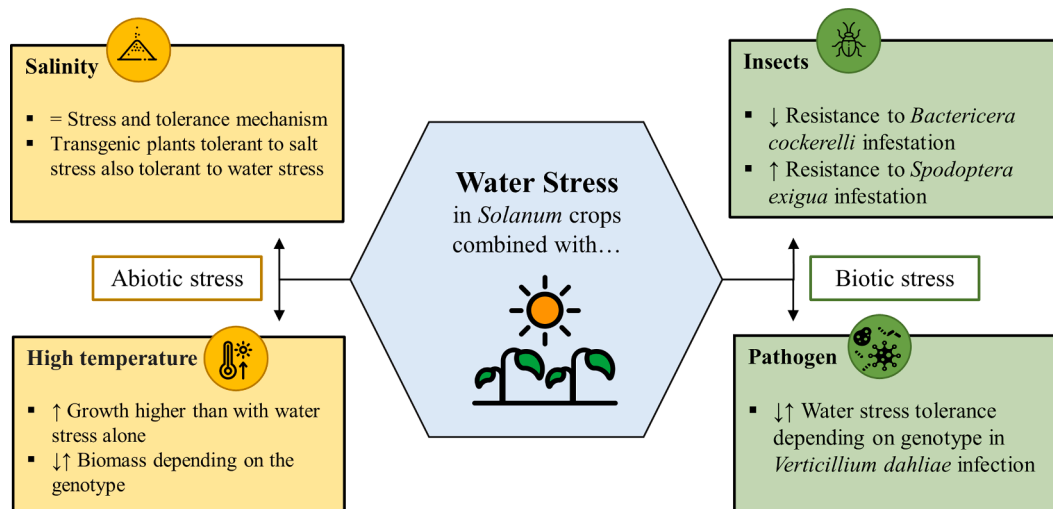


Fig. 1. Effects of water stress combined with biotic and abiotic stresses in *Solanum* crops. The symbols (↑) and (↓) mean a positive or negative effect on the susceptibility of the plant to water stress.

2.5. Advantages and disadvantages of stress induction methods

The different stress induction methods are very diverse, each of them presenting advantages and disadvantages for evaluation (Table 2). The space required for each method can vary greatly. For instance, using polyethylene glycol (PEG) in an *in vitro* culture setting requires less space, while inducing stress through withholding irrigation or reducing the percentage of evapotranspiration (ET) is typically done under field conditions (Amiri Rodan et al., 2020 and Semida et al., 2021) and requires more time, space, and resources (Table 1). Meanwhile, when using the method of reducing field capacity (FC) and withholding irrigation in a greenhouse setting, the area needed is typically smaller than in field conditions, but still larger than *in vitro* cultivation. Another important aspect to consider is the control of environmental parameters and the level of stress induced. When simulating water stress through PEG, the environmental conditions can be controlled and replicated, as well as the level of stress generated. However, in experimental designs involving reduced replenishment of field capacity or evapotranspiration, even though the water level remains constant and the substrate is controlled, the environmental conditions can be highly variable (Hochberg et al., 2017). In this sense, withholding irrigation is considered the most unstable and least replicable method, as the water level of the soil and environmental conditions can vary greatly.

Drought tolerance screening is for simulating real conditions of the crop at a commercial level. In this sense, the methods based on withholding irrigation or at certain levels of the FC or the ET can be performed at the field level or in greenhouses simulating a lower availability of daily irrigation (% of FC or ET), by a reduced frequency of irrigation or by irrigation withholding. Conversely, for water stress induction with PEG, although it decreases water availability for plants, the environmental conditions of *in vitro* culture and the use of germination chambers can be very different from real field conditions. Additionally, yield is generally not evaluable with this method, which is an important consideration for *Solanum* crops (Pino et al., 2013; Zayova et al., 2017;

Meng et al., 2020).

Another important aspect of the methodology used is the easiness and convenience of assessment. Withholding irrigation is the simplest method of inducing stress, followed by the application of PEG (Table 1). Lastly, the method of reduced replacement of FC or ET requires greater irrigation control, often on a daily basis during the experimental period (Szalonek et al., 2015; Martínez-Cuenca et al., 2020).

3. Water stress combined with other factors

3.1. Water stress combined with other stresses

The increasing prevalence of multiple stressors on plants, particularly in the context of climate change, makes studying the combined effects of these stresses increasingly important (Mahalingam, 2015). Research has shown that in *Solanum* crops, the presence of multiple stressors, including water stress, does not always lead to an exacerbation of negative effects and largely depends on the specific genotype under study (Fig. 1).

For abiotic stress, drought and salinity conditions generate a similar effect of stress and tolerance mechanisms in plants (Uddin et al., 2016). Due to this, the effects of water and saline stress are often studied together. Studies observed that within the genus *Solanum*, plants are negatively affected by saline conditions (Abdel-Farid et al., 2020; Jaarsma et al., 2013) and water limitations (Díaz-Pérez and Eaton, 2015; Rady et al., 2020). However, important advances were made in genetic regulation that allows greater tolerance to both salt and water stress, through the generation of transgenic plants (Choi et al., 2011; Goel et al., 2010; Waseem et al., 2019; Zhu et al., 2014). On the other hand, when combining hydric and high temperature stresses in tomato, it was observed a positive effect on plant height and the number of leaves; however, the biomass can be higher or lower when compared to heat stress alone, depending on the genotype (Blanchard-Gros et al., 2021).

Adverse weather conditions, such as drought, can make plants more

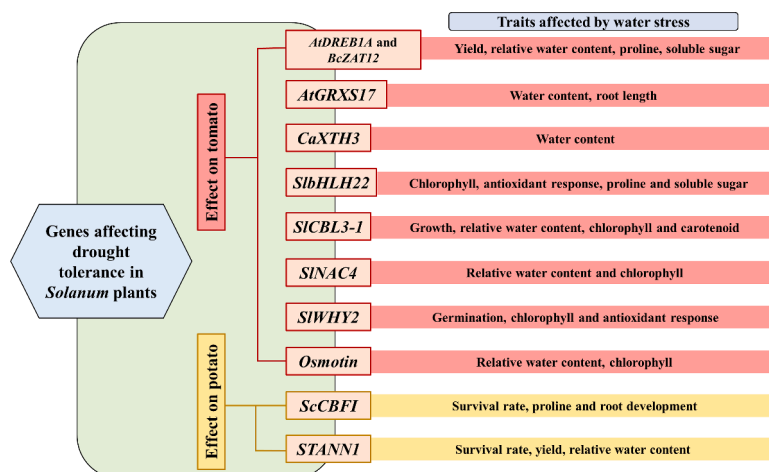


Fig. 2. Genes involved in drought tolerance in tomato or potato plants and their effects.

vulnerable to biotic stressors, such as pests and diseases (Teshome et al., 2020). Studies have also investigated the combined effects of drought and damage caused by insects and pathogens. For example, research has shown that tomato plants under water stress conditions are more susceptible to infestations by *Bactericera cockerelli*, with greater numbers of nymphs observed than in well-irrigated plants (Huot and Tamborindeguy, 2017). However, in some cases, such as in *S. dulcamara*, the combined stress of drought and the insect *Spodoptera exigua*, resulted in improved resistance to herbivores (Nguyen et al., 2016). In eggplant, the combined stress of drought and *Verticillium dahliae* can have positive or negative effects depending on the genotype under study (Tani et al., 2018).

3.2. Water stress combined with biostimulants

Biostimulants can alleviate abiotic stress and, in consequence, are of interest for a more sustainable agriculture (Matthews et al., 2022). In this way, methods for inducing water stress in *Solanum* crops combined with the use of biostimulants have been investigated. In this way, the application of biostimulants in tomato, such as 4-Vita (Campobenedetto et al., 2021) and Eranthis (Sudiro et al., 2022), under limited irrigation conditions was reported to increase photosynthetic capacity, chlorophyll content and response to oxidative stress. However, their positive effect on yield remains unproven (Top et al., 2023) and fruit quality responds differently to each biostimulant (Fernandes et al., 2022). Promising results were also observed in potato, where the application of the biostimulant clove fruit extract (CFE) improved the antioxidant response, growth and yield of tubers under water stress (Desoky et al., 2021). Despite the lack of research on the effects of biostimulants under water stress in eggplant, it was observed that the application of *Ascophyllum nodosum* standardised extract (Göemer BM-86) increased yield and fruit quality under field conditions (Pohl et al., 2019), making it a promising tool to evaluate the stress mitigation under drought conditions.

4. Traits evaluated under water stress conditions

4.1. Growth and biomass

Water stress in plants can greatly reduce their growth rate due to a decrease in water potential and transpiration rate, which leads to a reduction in cell turgor. As a result, important plant characteristics such as height, leaf area index, biomass, and yield are negatively impacted (Imadi et al., 2016).

4.1.1. Germination and survival of seedlings

The availability of water greatly affects the germination and survival of seedlings. However, there are significant variations depending on the genotype studied. For example, Easan et al. (2018) found that tomato germination was slightly reduced when exposed to a solution with 4% PEG, and in more severe stress conditions with 14% PEG, germination percentages were severely reduced and some seeds did not germinate at all. Meng et al. (2020) evaluated transgenic and wild-type tomato seedlings under water stress conditions simulated by 100 mM and 200 mM mannitol. Germination percentages decreased in both cases, but more significantly in the transgenic lines with silenced *SIWHY2* gene (Fig. 2). In potato, it was observed that transgenic seedlings expressing the *ScCBFI* gene were less affected by severe water stress and had a higher percentage of survival (around 100%) *in vitro* conditions than wild-type plants (which had a 40% reduction in survival) (Pino et al., 2013) (Fig. 2). Similarly, transgenic plants expressing the *STANN1* gene under water stress had a survival rate of 82% compared to 12% for wild-type plants (Szalonek et al., 2015) (Fig. 2). When evaluating the effect of water stress on eggplant *in vitro*, the percentage of live explants was not significantly affected when cultured with 10% PEG (Siaga et al., 2016). However, Zayova et al. (2017) found that plants were severely affected when exposed to the same level of stress (10% PEG for 21 days), with survival percentages ranging from 10% to 0% depending on the variety, while with 8% PEG, the effect was less severe with survival percentages ranging from 60% to 40%.

4.1.2. Plant height and foliar and root development

In tomato, a lack of water can significantly affect the plant's height (Bian et al., 2019; Hosseini Tafreshi et al., 2021). Additionally, stem diameter is one of the growth parameters that is commonly affected by water stress (Albert et al., 2016). However, other studies have not found significant differences for this trait (Landi et al., 2016; Tamburino et al., 2017), or in the number of nodes affected (Tamburino et al., 2017). In contrast, leaf development is clearly impacted by water deficit in tomato plants. The number of leaves decreases by approximately 28% in plants at the end of the cultivation period (Rady et al., 2020), and the leaf area is reduced following a decrease in irrigation (Bian et al., 2019; Chakna et al., 2021; Albert et al., 2016).

The height of potato plants decreases when irrigation is reduced, as observed by della Costa et al. (1997) and confirmed by Pino et al. (2013), even in genotypes with higher stress tolerance. Rolando et al. (2015) also found that length and vegetation cover are reduced with a decrease in water supply, with reductions of 25% and 43%, respectively.

Similarly, when evaluating the effects of water stress on eggplant *in vitro* culture, the height decreases significantly when PEG is added at 8% (Zayova et al., 2017). However, other studies under *in vitro* conditions

Table 3
Biomass and growth variables evaluated under water stress conditions.

Species	Growth and biomass measurements	References
<i>S. lycopersicum</i>	Root and shoot length, root and shoot weight	Kulkarni and Desphande (2010)
	Visual symptoms	Goel et al. (2010)
	Visual symptoms	Choi et al. (2011)
	Visual symptoms	Zhu et al. (2014)
	Height	Landi et al. (2016)
	Visual symptoms	Mishra et al. (2016)
	Height, number of knots, dry and fresh weight	Tamburino et al. (2017)
	Visual symptoms and root length	Wu et al. (2017)
	Germination percentage, root and shoot length, fresh weight.	Esan et al. (2018)
	Visual symptoms	Karkute et al. (2018)
	Height, leaf area and dry weight	Bian et al. (2019)
	Visual symptoms	Waseem et al. (2019)
	Visual symptoms	Akbudak et al. (2020)
	Visual symptoms	Filiz and Akbudak (2020)
	Visual signs, germination percentage and fresh weight	Meng et al. (2020)
	Number of leaves, fresh and dry weight, fruit weight, number of fruits and yield	Rady et al. (2020)
	Dry weight, yield	Takács et al. (2020)
	Fresh and dry weight	Azizi et al. (2021)
	Height, leaf area, dry weight, number of fruits, length of the fruit and yield.	Chakma et al. (2021)
	Leaf mass area	Galmés et al. (2013)
Height, fresh weight, root length	Hosseini Tafreshi et al. (2021)	
<i>S. tuberosum</i>	Fresh weight, root length, fruit weight, number of fruits and yield.	Krishna et al. (2021)
	Visual symptoms	Kappachery et al. (2013)
	Height, dry weight, tuber weight, tuber number and yield	della Costa et al. (1997)
	Tuber number, size and yield	Schafleitner et al. (2007)
	Yield	Boguszewska et al. (2010)
<i>S. kurtzianum</i>	Plant survival, height, foliage weight, length, diameter and root area	Pino et al. (2013)
	Leaf length, plant cover, aboveground dry weight, tuber dry weight	Rolando et al. (2015)
	Visual symptoms, plant survivals and yield	Szalonek et al. (2015)
	Height, total biomass, leaf biomass, leaflet thickness, tuber number and yield	Ibañez et al. (2021)
	Leaf area, dry weight, fruit weight, length and width of fruit, yield	Çolak et al. (2015)
<i>S. melongena</i>	Height, stem diameter, dry weight, number of fruits, yield	Díaz-Pérez y Eaton (2015)
	Percentage explants live, height, number of leaves, percentage explants callus	Siaga et al. (2016)
	Survived plants, rooted plants, height, root length	Zayova et al. (2017)
	Stem and root length, fresh and dry shoot/root weight ratio	Tani et al. (2018)
	Height, fresh weight	Plazas et al. (2019)
	Yield	Amiri Rodan et al. (2020)
	Height, number of leaves, stem diameter, dry and fresh weight, leaf area, fruit length, number of fruits, fruit weight, yield	Semida et al. (2021)
	Leaf area, dry weight, surface area, density and root length	Delfin et al. (2021)

did not find an effect on the number of leaves or shoot height when PEG is added at 10% (Siaga et al., 2016). Under greenhouse conditions, eggplant is affected by decreased irrigation, with stem growth rates in stressed plants being significantly lower than in well-watered plants (Tani et al., 2018). Severe water stress conditions can result in the growth of the plant in height being up to seven-fold lower than in non-stressed conditions (Plazas et al., 2019). In trials evaluating plants at the end of the crop cycle, height was found to be reduced by 16% (Semida et al., 2021), although Díaz-Pérez and Eaton (2015) did not find an effect of irrigation level on plant growth. The leaf area of eggplant is also affected by water stress, with reductions of 37% (Çolak et al., 2015), 27% (Semida et al., 2021), and 28% (Delfin et al., 2021) under water stress conditions.

Regarding root length, it decreases under water stress conditions in tomato plants (Esan et al., 2018). However, genotypes with greater tolerance have a greater root length compared to susceptible genotypes (Kulkarni and Deshpande, 2010). Advances in root development have also been made through transgenesis, where tomato plants expressing the *AtGRXS17* gene had a longer tap root than WT plants under water stress conditions (Wu et al., 2017) (Fig. 2). In tolerant potato genotypes expressing the *ScCBFI* gene, root length and area increase under moderate stress conditions (Fig. 2), but decrease under severe stress conditions for both tolerant and susceptible genotypes (Pino et al., 2013). Root growth in eggplant was found to be susceptible to water stress, as two genotypes evaluated under water stress showed reductions in length, biomass, and water content (Plazas et al., 2022).

4.1.3. Biomass production

The effects of water stress on growth and biomass in tomato have been widely studied, with a focus on characterizing gene function or gene expression (Wu et al., 2017; Akbudak et al., 2020). Typically, these studies have been conducted using visual inspections of wilting symptoms (Table 3). Although Tamburino et al. (2017) did not observe significant differences between stressed and control tomato plants for biomass fresh weight, many other studies reported opposite evidence ((Azizi et al., 2021; Rady et al., 2020; Tackács et al., 2020; Meng et al., 2020) as well as for biomass dry weight (Bian et al., 2019; Rady et al., 2020; Azizi et al., 2021; Chakma et al., 2021). For this parameter, it was reported that plants in which the gene *SLCBL3-I* is silenced have an even greater loss of growth under water stress conditions (Hosseini Tafreshi et al., 2021) (Fig. 2).

Potato biomass is also affected by water stress, with reductions of up to 92% under severe conditions (Pino et al., 2013). Tolerant transgenic plants with the *ScCBFI* gene were found to experience a lesser reduction (52%) in fresh weight. Similarly, Rolando et al. (2015) observed a decrease in aerial fresh and dry weight in stressed plants (36% compared to control plants). However, leaf dry weight was not affected to the same extent (della Costa et al., 1997). In eggplant, water stress has a significant impact on fresh weight, with the most affected organs being leaves and roots (Plazas et al., 2019). Studies have shown reductions in both fresh (26% reduction, Semida et al., 2021) and dry (24% reduction, Semida et al., 2021; 52% reduction, Çolak et al., 2015) weight. Additionally, water-stressed plants have been found to increase their root-to-shoot ratio (Delfin et al., 2021; Tani et al., 2018).

Overall, it is clear that the biomass of *Solanum* crops is affected by

water stress. The extent of the reduction varies depending on the species and genotype, with some genotypes displaying a higher level of tolerance. These differences in biomass loss could be attributed to variations in environmental conditions or inherent genetic differences.

4.1.4. Yield and yield components

Drought has a negative impact on food production worldwide and is widely recognized as the most influential abiotic stress in terms of yield loss (Begna, 2020). The effect of water deficit on tomato yield varies, with greater or lesser losses depending on the level of stress applied. For example, Rady et al. (2020) found decreases of between 62% and 69% for water stress conditions, depending on the season. Similarly, Tackás et al. (2020) found slight decreases of 16% and 25% when irrigating at 75% FC, and from 24% to 42% at 50% FC, depending on the year evaluated. Chakma et al. (2021) evaluated the performance at 100%, 75% and 50% FC, observing reductions in yield of 19% and 94% for 75% and 50% FC, respectively. In terms of transgenic plants, Krishna et al. (2021), evaluated double-transgenic plants for *AtDREB1A* and *BcZAT12*, finding that the double-transgenic plants presented a higher yield compared to individual ones and the control under water stress (Fig. 2). The decrease in yield is usually due to a decrease in the number of fruits per plant and the weight of the fruit (Rady et al., 2020; Chakma et al., 2021; Krishna et al., 2021). However, it is worth noting that the water deficit often leads to an increase in fruit quality (Albert et al., 2016).

Potato tuber yield is also affected by water scarcity, with a decrease of 84%, 72% and 58% when cultivated at 80%, 60% and 40% of their irrigation needs (della Costa et al., 1997). Boguszewska et al. (2010) found percentages of decrease in yield ranging from approximately 25% to 58% when evaluating 10 genotypes under water stress conditions, while Rolando et al. (2015) observed a 59% decrease when irrigating at 50% FC. On the other hand, Schafleitner et al. (2007) found yield losses that averaged around 50% when withholding the water supply, observing genotypes that combined moderate decreases with high yield potential. In the case of transgenic plants (*STANN1* gene), Szalonek et al. (2015) found improvements in yield quality under well-irrigated conditions and a slight decrease under water stress compared with WT plants, which had a decreased yield by half. The effects of drought stress on yield components vary depending on the genotype studied, so in some cases, the yield loss is due to the tuber weight, number of tubers or both (Schafleitner et al., 2007). It was also found that the weight of the tubers is promoted when plants are grown at 80% of the ET and not at 100% ET, but in more stressful conditions considerably decrease the weight. In relation to the number of tubers, these are affected by stress to a greater extent than those of larger size (della Costa et al., 1997).

Like tomato and potato, eggplant yield is negatively affected by water scarcity (Díaz-Pérez and Eaton, 2015), although the losses are not as severe. In a study by Semida et al. (2021), a 17% decrease in yield was found when irrigation was at 60% ETc. Amiri Rodan et al. (2020) found an even greater decrease in yield of 32% under more restrictive irrigation at 40% ETc, while Çolak et al. (2015) reported losses of up to 49%. The weight of the fruits, as well as their length and width, were all affected by water stress, with decreases of 13%, 17%, and 23%, respectively (Çolak et al., 2015). The number of fruits was also impacted by water stress and had a stronger correlation with yield than fruit weight (Díaz-Pérez and Eaton, 2015). However, Semida et al. (2021) found that the majority of the yield loss was due to a reduction in the weight of the fruits, rather than the number of fruits.

4.2. Physiological and biochemical traits

One of the first responses of plants to water stress is to close their stomata. This triggers several effects on physiological and biochemical processes, such as adjustments to the photosynthetic system, accumulation of osmolytes, and a number of mechanisms aimed at overcoming the period of water limitation (Kapoor et al., 2020). In addition to this, water stress also causes oxidative stress in plants, leading to an increase

in the production of reactive oxygen species, which ultimately leads to cell death, as well as an increase in the production of antioxidant enzymes as a response to water stress (Mattos and Moretti, 2016). Among *Solanum* species, tomato has the most documented information on the biochemical and physiological processes that occur during water stress.

4.2.1. Water content

Drought causes a significant reduction in the relative water content (RWC) of tomato plants (Bian et al., 2019). Reductions of 22% were observed when irrigated at 60% FC (Rady et al., 2020) and 13% when irrigated at 50% FC (Azizi et al., 2021). Chakma et al. (2021) also found decreases in RWC when applying lower amounts of water, although the decreases were not as significant. The decrease in RWC is related to a decrease in water potential and lower plant productivity, as reported by Nunes et al. (2022). To address this issue, scientists have developed transgenic plants that can increase RWC under conditions of limited water (Fig. 2). For example, Goel et al. (2010) reported higher RWC values in some modified lines overexpressing the *osmotin* gene. In addition, Krishna et al. (2021) evaluated double transgenic plants of *AtDREB1A* and *BcZAT12* exposed to 21 days of water deficit and observed that RWC was less affected than in WT plants. On the other hand, the functionality of genes involved in drought tolerance was assessed by silencing them. In this way, Zhu et al. (2014), when evaluating plants in which the *SINAC4* gene had been silenced, found that the RWC decreased to a greater extent after 15 and 21 days of treatment than in the WT lines. On the other hand, Hosseini Tafreshi et al. (2021) observed that tomato plants with transient silencing of the *SICBL3-1* gene had a higher RWC than non-silenced plants when grown under water stress conditions. Another way to assess the hydration status of leaves is to determine the loss of water content in the leaf by subtracting the weight of the leaf material at the time of detachment from the plant from the initial fresh weight of the leaf. Using this method, Choi et al. (2011) saw a 13% weight loss after 10 min, while resistant transgenic plants (*CaXTH3*) only lost between 3.4% and 4.7% of their weight. In addition, transgenic lines expressing the *AtGRXS17* gene were found to have higher water content than WT plants (Wu et al., 2017).

In potato, when evaluating ten genotypes under water stress, it was observed that RWC decreased between 45% and 65% with respect to well-watered plants, but this decrease did not correlate with the loss of yield under stress (Boguszewska et al., 2010). Similarly, in the wild relative *S. kurtzianum*, the RWC decreased when water availability was lower (Ibañez et al., 2021). Through biotechnological approaches, advances were made in this aspect. In this way, when evaluating transformed potato plants with overexpression of the *STANN1* gene, after 12 days without irrigation, the RWC was higher than that of WT plants (Szalonek et al., 2015) (Fig. 2).

Similarly, in eggplant, water stress also affects the water status of the plants, causing a decrease in RWC by 7% when subjected to a stress of 60% ETc (Semida et al., 2021). This reduction is less than that observed in tomato plants, indicating a higher tolerance to water stress in eggplant (Rady et al., 2020; Azizi et al., 2021). Additionally, the effect of water stress on the water potential of eggplant can also be seen through a decrease of -1.5 MPa when cultivated with up to 10% of the field capacity replacement (Delfin et al., 2021).

4.2.2. Gas exchange

Gas exchange parameters in tomato are affected by hydric stress conditions. Drought causes a decrease in photosynthesis and stomatal conductance a few days after the stress is imposed, with mesophyll conductance being subsequently affected (Bian et al., 2019). Photosynthesis in well-irrigated tomato plants ranges between 15.6 and 20.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is significantly reduced under stress conditions, with values ranging between 1.5 and 10.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Similarly, mesophyll conductance varies between 0.17 and 0.29 $\text{mol m}^{-2} \text{s}^{-1}$ under well-irrigated conditions, while under stress, values range from 0.02 to 0.13 $\text{mol m}^{-2} \text{s}^{-1}$ (Galmés et al., 2013). Landi et al. (2016)

evaluated stomatal conductance of tomato under hydroponic, greenhouse, and field conditions and found a strong effect of water stress in hydroponically grown plants exposed to PEG, with stomatal conductance values decreasing by 72%. In the case of greenhouse plants, with the suspension of irrigation, stomatal conductance was reduced by 92%, and in field conditions, the difference was less marked, with a decrease of 43% after 45 days of withholding irrigation. Tamburino et al. (2017) also found an important effect of water stress in tomato, with values reduced by up to 98% compared to control plants, after 19 days of withholding irrigation. The intrinsic and instantaneous water use efficiency (WUE), calculated as the ratio between photosynthesis and stomatal conductance and the ratio between photosynthesis and transpiration rate, respectively, shows a significant increase in tomato plants under water stress, with a trend of increasing values as days of withholding irrigation pass (Bian et al., 2019).

Like tomato, potato also experiences a decrease in photosynthesis and stomatal conductance under water stress conditions, while the instantaneous WUE increases (Rolando et al., 2015). Similarly, in the wild parent, *S. kurtzianum* water stress decreases stomatal conductance, although genotypes were found to be less affected than others (Ibañez et al., 2021). It is important to note that stomatal conductance cannot be used as a reliable indicator of yield under water-limited conditions, as stomatal resistance does not necessarily correlate with higher yield under stress (Schafleitner et al., 2007). Studies have also shown that in water-stress tolerant potato plants overexpressing the *STANNI* gene, their photosynthetic rate and stomatal conductance decrease when exposed to water stress, just like WT plants (Szalonek et al., 2015).

In eggplant, gas exchange shows a drastic decrease in photosynthetic rate, stomatal conductance and transpiration under water stress, with decreases of 73%, 88% and 82%, respectively. However, the intrinsic WUE, increases by 48% under stress conditions (Delfin et al., 2021). Tani et al. (2018) found that when evaluating two different genotypes, the levels of gas exchange (photosynthesis, stomatal conductance, transpiration, and CO₂ concentration) decreased significantly under water stress conditions (25% field capacity), while the instantaneous and intrinsic WUE increased. On the other hand, Díaz-Pérez and Eaton (2015), saw that when the temperature is lower, there were no differences in photosynthesis, stomatal conductance, and WUE resulting in a low evapotranspiration demand. However, under conditions of higher temperature, photosynthesis and stomatal conductance decrease due to less water availability.

In *Solanum* crops, a clear trend is observed where the gas exchange parameters decrease in a water stress condition, while the WUE increases. Although an increase in WUE might suggest greater tolerance to stress, it is not always related to reaching higher yields when the plants are grown in limited water conditions. This is because if the plant cannot maintain adequate levels of carbon gain, biomass production will be low, regardless of whether WUE is increased through stomatal closure (Leakey et al., 2019).

4.2.3. Photosynthetic pigments

Chlorophyll is the primary pigment responsible for photosynthesis in plants, and its levels have been found to decrease under water stress conditions in tomato plants (Hosseini Tafreshi et al., 2021). However, some studies have not found significant differences in chlorophyll levels after withholding irrigation for 19 days (Tamburino et al., 2017) or only slight decreases when using PEG application (Karaca and Cekic, 2019). When evaluating the chlorophyll content using a portable chlorophyll meter (SPAD), it was found that it was reduced between 25% and 23% when tomato was irrigated to 60% of the FC (Rady et al., 2020), while Chakma et al. (2021), when evaluating the chlorophyll content in the same way, it was reduced by 8% when it was irrigated to 50% FC. By evaluating transgenic tomato plants, significant effects on chlorophyll content were observed (Fig. 2). In this way, when evaluating plants tolerant to water stress, which overexpress the osmotin gene, it was seen that chlorophyll levels increase by approximately 50% under limited

water conditions (Goel et al., 2010). Additionally, transgenic plants with overexpression of the *SibHLH22* gene have been found to maintain chlorophyll levels four times higher than WT plants when subjected to severe stress for 30 days without irrigation (Waseem et al., 2019). On the other hand, transgenic plants with silencing of the *SINAC4* gene have been found to have a greater reduction in chlorophyll content under stress conditions than wild-type plants (Zhu et al., 2014). In the same way, when the *SICBL3-1* gene is silenced, the plant exhibited a greater reduction in chlorophyll and carotenoid content under water stress conditions (Hosseini Tafreshi et al., 2021). Similarly, CRISPR-edited plants with the *SLWHY2* gene silenced have also been found to be more affected than non-transgenic plants, with chlorophyll levels decreasing by around 30% (Meng et al., 2020).

In potato plants, water stress has been found to have varying effects on photosynthetic pigments. Some studies have found that SPAD values, which measure chlorophyll content, are higher under water stress conditions than in control conditions (Rolando et al., 2015). However, other studies have not found a significant increase in chlorophylls *a* and *b* when plants are subjected to 14 days without irrigation (Szalonek et al., 2015). In water-stressed *S. kurtzianum* plants, it has been observed that the content of chlorophyll and carotenoids decreases significantly under severe stress conditions (Ibañez et al., 2021).

In eggplant, research has found that chlorophyll *a*, chlorophyll *b*, and carotenoids decrease in content when the plants are exposed to severe water stress. These photosynthetic pigments also display a positive correlation with biomass levels (Plazas et al., 2019). Under moderate water stress conditions, a trend towards a reduction in carotenoids has also been reported (Amiri Rodan et al., 2020), while chlorophylls, as measured by a SPAD meter, tend to increase (Díaz-Pérez and Eaton, 2015).

When comparing results from different studies, it is clear that the effects of water stress on photosynthetic pigments can vary greatly. The way in which the results are expressed, such as in mg of chlorophyll per g of fresh weight or dry weight, or as a chlorophyll index when using a SPAD meter, can also play a decisive role. Additionally, the results, when expressed in fresh weight or using a SPAD meter, do not take into account the effect of nutrient dilution that occurs when comparing irrigated plants to those under water stress. Therefore, to accurately evaluate the effects of stress on photosynthetic pigments, it is best to express the values in dry weight, although this method is not commonly used in research articles (Plazas et al., 2019; Ibañez et al., 2021).

4.2.4. Oxidative stress

To assess the effect of drought on oxidative stress in tomato, measurements of the content of malondialdehyde (MDA), hydrogen peroxide (H₂O₂) and superoxide (O₂⁻) are used as biomarkers, where they generally increase their concentration under water stress conditions (Rady et al., 2020). Several studies have reported oxidative stress in tomato plants exposed to different levels of water stress and genotypes. For instance, Akbudak et al. (2020) observed that the contents of H₂O₂ and MDA increased by more than 100% in plants that were stressed for 10 days without irrigation. Similarly, Krishna et al. (2021) found that the concentration of H₂O₂ increased as the stress level increased, with values more than two-fold higher in plants that were stressed for 21 days compared to control plants. When comparing tolerant and susceptible genotypes, it was found that the MDA and H₂O₂ content increased in both, but the increase was lower in the tolerant genotypes (Hosseini Tafreshi et al., 2021). Additionally, Meng et al. (2020) reported an increase in H₂O₂ and O₂⁻ levels in tomato plants stressed with PEG. However, when evaluating the oxidative stress levels in leaves and roots separately, Filiz and Akbudak (2020) found that the H₂O₂ and MDA changes were only significant in the leaves and not in the roots. An increase in MDA content indicates a higher level of oxidative stress that can be induced by lack of water, which correlates with a lower level of growth; however, there are eggplant genotypes that are able to maintain their MDA levels under water stress conditions, which is

evidence that they are not affected by oxidative stress (Plazas et al., 2019). Contrary to these results, Tani et al. (2018), when evaluating two different genotypes, found a significant increase in H₂O₂ and MDA, showing a significant effect of oxidative stress induced by decreased irrigation.

To defend against oxidative stress, plants increase the activity of antioxidant enzymes. For example, in tomato plants, researchers have seen increases in the activity of superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) (Rady et al., 2020). Nevertheless, there is a genotype effect, where more tolerant plants have greater antioxidant activity. Transgenic lines that are tolerant to water deficit (overexpression of the *SibHLH22* gene) have been found to have greater CAT and peroxidase (POD) activity compared to sensitive wild-type plants (Waseem et al., 2019) (Fig. 2). On the other hand, Meng et al. (2020) found that the more resistant genotypes had a significant increase in alternative protein oxidase (AOX) content, while susceptible plants with the *SIWHY2* gene silenced had lower AOX content than wild-type plants with higher tolerance to water stress (Fig. 2). Hosseini Tafreshi et al. (2021) found that antioxidant enzyme activities increased under water stress conditions, with SOD and APX increasing in both susceptible and drought-resistant plants, and CAT activity only increasing in resistant plants, which suggests that CAT could be an important enzyme to consider when searching for resistant genotypes. Karaca and Cekic (2019) did not find clear differences in the activity of SOD, APX, and glutathione reductase (GR) when comparing plants stressed with PEG and control plants. This is in contrast to the other studies mentioned where a significant increase in enzyme activity was observed, indicating that the plant material or stress level could have had an important effect in this case. In potato, researchers have found that when subjected to water stress conditions, the activity of SOD and POD increases as a defense against oxidative stress (Boguszewska et al., 2010). Similarly, in eggplant, an important defense mechanism against oxidative stress in plants is the enzymes SOD, CAT, and GR. For example, Amiri Rodan et al. (2020) evaluated SOD and GR and observed an increase in their activity when irrigation decreased. However, Plazas et al. (2019) found that when evaluating the enzymatic activity of the four enzymes under severe stress, only CAT increased, which may be due to a more severe and brief stress induction method and also to differences among the genotypes studied in each trial.

4.2.5. Osmoprotective compounds

As a response to drought, plants generate osmolytes in their

cytoplasm to maintain their physiological functions (Slama et al., 2015). One such osmolyte, proline, plays a key role as an osmoreceptor, helping to adjust osmotic pressure and reducing the effects of oxidative stress (Per et al., 2017). Proline is the most commonly tested osmoprotectant compound in trials of *Solanum* crops. In tomato plants, proline content was observed to increase up to 10 times when they were subjected to water stress (Landi et al., 2016). Similarly, Tamburino et al. (2017) found that proline content increased six-fold when plants were exposed to severe stress. Even under moderate water stress, a significant effect on proline content can be seen, as demonstrated by Rady et al. (2020), who found an increase of 19% when plants were irrigated with 60% FC. Genotypes that are more tolerant to water stress were found to have a greater increase in proline content than susceptible genotypes (Azizi et al., 2021; Hosseini Tafreshi et al., 2021). In this way, measuring this parameter can be useful in the selection of plant materials tolerant to restrictive water conditions. On the other hand, Krishna et al. (2021) generated double transgenic plants with the *AtdREB1A* and *BcZAT12* genes, while Waseem et al. (2019) generated plants with overexpression of *SibHLH22*, and in both studies, an increase in proline content was observed under water stress conditions (Fig. 2).

Plants with greater tolerance to drought conditions have been obtained through the overexpression of the *ScCBF1* gene in potato, which has been found to increase proline content under water stress conditions (Pino et al., 2013). In contrast, *S. kurtzianum* plants did not show an increase in proline content under moderate stress exhibited a dramatic increase under severe stress conditions. This may indicate that proline accumulation in these plants is not only a response to osmotic regulation but also a marker of high plant stress levels (Ibáñez et al., 2021).

The accumulation of proline in eggplant also seems to be an important indicator of the level of hydric stress, and various studies have found significant increases in water-stressed plants. In this way, Zayova et al. (2017) observed an increase under *in vitro* conditions by adding PEG, while Tani et al. (2018), found significant increases in the two genotypes studied. Similarly, Plazas et al. (2019) found dramatic increases in four genotypes studied and a negative correlation with biomass traits, while Amiri Rodan et al. (2020) did not find a clear increase when irrigating at 70% ETc, which indicates a non-stressful condition for the plants, however when irrigating at 40%, the increase in proline was significant.

The sugar content in plants is also considered an important component as an osmoprotectant under stress conditions (Ahmad et al., 2020; Halford et al., 2011). In tomato plants, it was found that the increase in

Table 4
Wild species of *Solanum* tolerant to water stress, geographical origin and precipitation.

Species	Genotype	Geographical location	Precipitation (mm)	Reference
Tomato				
<i>S. pimpinellifolium</i>	Pim2	Piura, Peru	49,0	Martínez-Cuenca et al. (2020)
<i>S. pimpinellifolium</i>	Pim3	Amazonas, Peru	732,0	Martínez-Cuenca et al. (2020)
<i>S. lycopersicum</i> var. <i>cerasiforme</i>	Ceras1	Sinaloa, Mexico	341,0	Martínez-Cuenca et al. (2020)
<i>S. chilense</i>	LA1958	Moquegua, Peru	6,0	Blanchard-Gros et al. (2021)
<i>S. chilense</i>	LA2765	Arica and Parinacota, Chile	51,0	Blanchard-Gros et al. (2021)
<i>S. chilense</i>	LA2880	Antofagasta, Chile	36,0	Blanchard-Gros et al. (2021)
<i>S. chilense</i>	LA4107	Antofagasta, Chile	22,0	Blanchard-Gros et al. (2021)
<i>S. peruvianum</i>	Q958	Tarapaca, Chile	0,5	Tapia et al. (2016)
<i>S. peruvianum</i>	Q962	Tarapaca, Chile	0,4	Tapia et al. (2016)
<i>S. pennelli</i>	PE47	Peru	–	Egea et al. (2018)
Potato				
<i>S. kurtzianum</i>	G1	Mendoza, Argentina	–	Ibáñez et al. (2021)
<i>S. kurtzianum</i>	G2	Mendoza, Argentina	–	Ibáñez et al. (2021)
<i>S. kurtzianum</i>	G3	Mendoza, Argentina	–	Ibáñez et al. (2021)
<i>S. commersonii</i>	–	Argentina, Brazil and Uruguay	–	Pino et al. (2013)
Eggplant				
<i>S. incanum</i>	MM577	Israel	–	Plazas et al. (2022)
<i>S. incanum</i>	INC1	Israel	–	Plazas et al. (2022)
<i>S. pyracanthos</i>	PYR1	USA	–	Plazas et al. (2022)
<i>S. dasyphyllum</i>	DAS1	Uganda	–	Plazas et al. (2022); Villanueva et al. (2023)
<i>S. torvum</i>	TOR3	France	–	Plazas et al. (2022)

the content of soluble sugars contributed to the optimal state of the leaf tissue in conditions of water stress (Rady et al., 2020). Likewise, through biotechnological tools, increases in the content of soluble sugars were achieved (Waseem et al., 2019; Krishna et al., 2021) (Fig. 2).

4.3. Next-generation phenotyping methods

High-throughput phenotyping greatly facilitates the evaluation of complex traits of interest (Singh et al., 2016), providing a powerful tool for identifying genotypes tolerant to water stress through the use of technologies such as red, green and blue (RGB) imaging, infrared imaging, hyperspectral imaging, thermal imaging, fluorescence imaging and light detection and ranging (LiDAR) (Kim et al., 2020). The use of these new technologies has not been extensively studied in *Solanum* crops, so it will be essential to incorporate them in the development of new *Solanum* cultivars capable of growing under conditions of low water availability. In this sense, UAVs' remote sensing was applied in tomato grown under drought conditions, where physiological and quality characteristics of the fruit can be associated with multispectral indices (Fullana-Pericàs et al., 2022). In addition, by using proximal sensing and multispectral UAV imagery allowed monitoring of the plant water status of tomato plants, allowing more precise irrigation management (Tang et al., 2023). Meanwhile, in potato, the assessment of large populations has been achieved using infrared thermography and is postulated as a method of great interest for assessment under drought (Prashr et al., 2013).

5. Wild species

Wild species of the genus *Solanum* have been a valuable source of genes for improving crops such as tomato (Kulus, 2018), potato (Machida-Hirano and Niino, 2017) and eggplant (Plazas et al., 2016; Oladosu et al., 2021). However, using wild parents in plant breeding can be challenging due to the potential transfer of undesirable traits. Biotechnological approaches can help overcome this issue (Ford-Lloyd et al., 2011). Quantitative trait loci (QTLs) for drought tolerance have been identified in wild species of important crops such as wheat, barley, and tomato, but their effective introgression into crops is difficult due to the polygenic inheritance of tolerance (Majeed et al., 2021).

Wild tomato relatives such as *S. pimpinellifolium*, *S. chilense* or *S. peruvianum* are an important genetic resource for improving tolerance to water stress (Table 4); however, it was found that genotypes harvested under lower rainfall conditions are not always the most tolerant (Martínez-Cuenca et al., 2020; Blanchard-Gros et al., 2021). In particular, accessions of *S. pimpinellifolium* and *S. lycopersicum* var. *cerasiforme* that have adapted well to water deficit were found to have minimal effects on agronomic, morphological, and gas exchange traits. For example, drought-tolerant genotypes from *S. pimpinellifolium* were collected from a desert area on the coast of Peru, while *S. lycopersicum* var. *cerasiforme* were collected from the Sinaloa desert in Mexico (Martínez-Cuenca et al., 2020). In *S. chilense*, accessions that were both sensitive and resistant to water stress were found, with the most resistant accessions characterized by slower growth and increased proline and MDA content (Blanchard-Gros et al., 2021). Tapia et al. (2016) found an increase in proline content in *S. chilense* and an increase in total carbohydrates in *S. peruvianum* that correlate with a higher osmotic potential that allows growth under stress conditions. Additionally, the wild species *S. pennellii* is known to have a greater tolerance to water stress conditions compared to the cultivated tomato, due to its ability to decrease water losses through stomatal regulation and reduce oxidative damage (Egea et al., 2018).

Regarding potato, the wild relative *S. kurtzianum* exhibited tolerance to moderate water stress, as genotypes were found to be unaffected in terms of plant height, tuber weight, and the number of tubers (Ibañez et al., 2021). On the other hand, through the overexpression of the *ScCBFI* gene from the wild species of potato *S. commersonii*, which is

native to Argentina, Brazil and Uruguay (de Haan and Rodriguez, 2016), greater tolerance to water stress was observed in potato (Pino et al., 2013).

As for wild parents of eggplant, under severe water stress, the species *S. incanum*, *S. pyracanthos*, *S. dasyphyllum*, and *S. torvum* were identified as tolerant (Plazas et al., 2022). These genotypes demonstrated decreased aerial dry weight by less than 25%, an increase in proline content, the ability to maintain MDA levels, and an increase in flavonoid content. In addition, *S. dasyphyllum*, when subjected to osmotic stress, showed higher tolerance and a differential response at the transcriptomic level, indicating that it is a potential source for abiotic stress amelioration (Villanueva et al., 2023).

Introgression breeding with crop wild relatives, such as the development of introgression lines (ILs), is a powerful tool that allows identifying genes and QTLs for breeding (Lippman et al., 2007; Zhang et al., 2021). In this sense, ILs have been used to introduce regions from the wild relatives into cultivated species, as in the case of Poudyal et al. (2017) who generated rootstocks with *S. habrochaites* introgression that improved tomato growth under drought. Tomato lines with *S. pennellii* introgressions have also been generated with greater water use efficiency (Galdon-Armero et al., 2018). Similarly, Fenstemaker et al. (2022) developed an inbred backcross (IBC) population by crossing *S. galapagense* with tomato where identified lines with greater maintenance of cell turgor under water stress conditions. Also in eggplant, an introgression line has been generated with the wild relative *S. incanum*, a drought-tolerant species, identifying a large number of candidate genes for drought tolerance (Gramazio et al., 2017).

6. Conclusions

The methods used to induce water stress in *Solanum* crops are diverse and include *in vitro* growth chamber, greenhouse and field conditions. This results in a range of different methods that provide different, but complementary, information on water stress tolerance in *Solanum* crops. However, the specific conditions for each method make comparisons with drought tolerance complex. Therefore, there is no optimal single standardized method for evaluating drought tolerance and it must be selected based on the environmental conditions and plant material being evaluated, as well as its correlation with real drought tolerance under commercial growing conditions. It is also important to consider other possible stresses, both biotic and abiotic, that may affect drought tolerance as well as the potential effect of biostimulant application to improve stress tolerance. Growth and yield of *Solanum* crops are negatively affected by reduced water availability, but the selection of genotypes with higher tolerance can result in a significant reduction in yield loss. The selection of more tolerant genotypes can lead to significant progress in the development of more drought-tolerant crops. In recent years, new phenotyping strategies have been developed that have great potential for identifying materials with greater tolerance to water stress in *Solanum* crops. In addition, the use of transgenics and CRISPR/Cas editing has shown promising results in tomato and potato crops, while high tolerance genotypes have been found in wild species, providing an opportunity to improve drought tolerance in cultivated *Solanum* species.

Funding

This work was supported by grant CIPROM/2021/020 from Conselleria d'Innovació, Universitats, Ciència i Societat Digital (Generalitat Valenciana, Spain) as well as by the Horizon Europe program, project "Promoting a Plant Genetic Resource Community for Europe (PRO-GRACE), project number n. 101,094,738. This study also forms part of the AGROALNEXT program and was supported by MCIN with funding from European Union NextGenerationEU (PRTR-C17.11) and by Generalitat Valenciana. Martín Flores is grateful to Conselleria d'Innovació, Ciència i Societat Digital de la Generalitat Valenciana for a pre-doctoral grant within the Santiago Grisolia program (GRISOLIAP/2021/151).

Pietro Gramazio is grateful to Spanish Ministerio de Ciencia e Innovación for a post-doctoral grant (RYC2021-031,999-I) funded by MCIN/AEI /10.13039/501,100,011,033 and the European Union through NextGenerationEU/PRTR.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pietro Gramazio reports financial support was provided by Spanish Ministerio de Ciencia e Innovación. Jaime Prohens reports financial support was provided by Generalitat Valenciana. Jaime Prohens reports financial support was provided by Horizon Europe program. Martin Flores reports financial support was provided by Generalitat Valenciana.

Data availability

No data was used for the research described in the article.

References

- Abdel-Farid, I.B., Marghany, M.R., Rowezek, M.M., Sheded, M.G., 2020. Effect of salinity stress on growth and metabolic profiling of *Cucumis sativus* and *Solanum lycopersicum*. *Plants* 9 (11), 1626. <https://doi.org/10.3390/plants9111626>.
- Ahmad, F., Singh, A., Kamal, A., 2020. Osmoprotective role of sugar in mitigating abiotic stress in plants. *Protective Chem. Agents Amelioration of Plant Abiotic Stress* 53–70. <https://doi.org/10.1002/9781119552154.ch3>.
- Akbudak, M.A., Yildiz, S., Filiz, E., 2020. Pathogenesis related protein-1 (PR-1) genes in tomato (*Solanum lycopersicum* L.): bioinformatics analyses and expression profiles in response to drought stress. *Genomics* 112 (6), 4089–4099. <https://doi.org/10.1016/j.ygeno.2020.07.004>.
- Aksoy, E., Demirel, U., Bakhsh, A., Zia, M.A.B., Naeem, M., Saeed, F., Çalışkan, S., Çalışkan, M.E., 2021. Recent Advances in Potato (*Solanum tuberosum* L.) Breeding. In: Al-Khayri, J.M., Jain, S.M., Johnson, D.V. (Eds.), *Advances in Plant Breeding Strategies: Vegetable Crops*. Springer, Cham, pp. 409–487. https://doi.org/10.1007/978-3-030-66965-2_10.
- Albert, E., Segura, V., Gricourt, J., Bonnefoi, J., Derivot, L., Causse, M., 2016. Association mapping reveals the genetic architecture of tomato response to water deficit: focus on major fruit quality traits. *J. Exp. Bot.* 67 (22), 6413–6430. <https://doi.org/10.1093/jxb/erw411>.
- Al-Taisan, W.A., Al-Qarawi, A.A., Alsubiee, M.S., 2010. Effect of water stress by Polyethylene Glycol 8000 and Sodium Chloride on germination of *Ephedra alata* Decne seeds. *Saudi J Biol Sci* 17 (3), 253–257. <https://doi.org/10.1016/j.sjbs.2010.04.011>.
- Amiri Rodan, M., Hassandokht, M.R., Sadeghzadeh-Ahari, D., Mousavi, A., 2020. Mitigation of drought stress in eggplant by date straw and plastic mulches. *J. Saudi Society of Agric. Sci.* 19 (7), 492–498. <https://doi.org/10.1016/j.jssas.2020.09.006>.
- Arnell, N.W., Lowe, J.A., Challinor, A.J., Osborn, T.J., 2019. Global and regional impacts of climate change at different levels of global temperature increase. *Clim. Change* 155 (3), 377–391. <https://doi.org/10.1007/s10584-019-02464-z>.
- Azizi, M., Fard, E.M., Ghabooli, M., 2021. *Piriformospora indica* affect drought tolerance by regulation of genes expression and some morphophysiological parameters in tomato (*Solanum lycopersicum* L.). *Sci. Hortic.* 287, 110260 <https://doi.org/10.1016/j.scienta.2021.110260>.
- Begna, T., 2020. Effects of Drought Stress on Crop Production and Productivity. *Int. J. Res. Stud. Agric. Sci.* 6 (9), 34–43. <https://doi.org/10.20431/2454-6224.0609005>.
- Bian, Z., Zhang, X., Wang, Y., Lu, C., 2019. Improving drought tolerance by altering the photosynthetic rate and stomatal aperture via green light in tomato (*Solanum lycopersicum* L.) seedlings under drought conditions. *Environ. Exp. Bot.* 167, 103844 <https://doi.org/10.1016/j.envexpbot.2019.103844>.
- Blanchard-Gros, R., Bigot, S., Martinez, J.P., Lutts, S., Guerriero, G., Quinet, M., 2021. Comparison of Drought and Heat Resistance Strategies among Six Populations of *Solanum chilense* and Two Cultivars of *Solanum lycopersicum*. *Plants* 10 (8), 1720. <https://doi.org/10.3390/plants10081720>.
- Boguszewska, D., Grudkowska, M., Zagdańska, B., 2010. Drought-Responsive Antioxidant Enzymes in Potato (*Solanum tuberosum* L.). *Potato Res* 53 (4), 373–382. <https://doi.org/10.1007/s11540-010-9178-6>.
- Campobenedetto, C., Agliassa, C., Mannino, G., Vigliante, I., Contartese, V., Secchi, F., Berte, C.M., 2021. A Biostimulant Based on Seaweed (*Ascopyllum nodosum* and *Laminaria digitata*) and Yeast Extracts Mitigates Water Stress Effects on Tomato (*Solanum lycopersicum* L.). *Agriculture* 11 (6), 557. <https://doi.org/10.3390/agriculture11060557>.
- Chakma, R., Biswas, A., Saekong, P., Ullah, H., Datta, A., 2021. Foliar application and seed priming of salicylic acid affect growth, fruit yield, and quality of grape tomato under drought stress. *Sci. Hortic.* 280, 109904 <https://doi.org/10.1016/j.scienta.2021.109904>.
- Choi, J.Y., Seo, Y.S., Kim, S.J., Kim, W.T., Shin, J.S., 2011. Constitutive expression of CaXTH3, a hot pepper xyloglucan endotransglucosylase/hydrolase, enhanced tolerance to salt and drought stresses without phenotypic defects in tomato plants (*Solanum lycopersicum* cv. Dotaerang). *Cell Rep* 30 (5), 867–877. <https://doi.org/10.1007/s00299-010-0989-3>.
- Christou, A., Daliass, P., Neocleous, D., 2017. Spatial and temporal variations in evapotranspiration and net water requirements of typical Mediterranean crops on the island of Cyprus. *J. Agric. Sci.* 155 (8), 1311–1323. <https://doi.org/10.1017/S0021859617000405>.
- Çolak, Y.B., Yazar, A., Çolak, L., Akça, H., Duraktekin, G., 2015. Evaluation of crop water stress index (CWSI) for eggplant under varying irrigation regimes using surface and subsurface drip systems. *Agric. Agric. Sci. Procedia* 4, 372–382. <https://doi.org/10.1016/j.aaspro.2015.03.042>.
- Cook, B.I., Mankin, J.S., Anchukaitis, K.J., 2018. Climate change and drought: from past to future. *Curr. Clim. Change Rep.* 4 (2), 164–179. <https://doi.org/10.1007/s40641-018-0093-2>.
- Dalla Costa, L., Delle Vedove, G., Gianquinto, G., Giovanardi, R., Peressotti, A., 1997. Yield, water use efficiency and nitrogen uptake in potato: influence of drought stress. *Potato Res.* 40 (1), 19–34. <https://doi.org/10.1007/bf02407559>.
- de Haan, S., Rodriguez, F., 2016. Chapter 1 - Potato Origin and Production. In: Singh, J., Kaur, L. (Eds.), *Advances in Potato Chemistry and Technology* (Second Edition). Academic Press, pp. 1–32. <https://doi.org/10.1016/b978-0-12-800002-1.00001-7>.
- Delfin, E.F., Drobnitch, S.T., Comas, L.H., 2021. Plant strategies for maximizing growth during water stress and subsequent recovery in *Solanum melongena* L. (eggplant). *PLoS ONE* 16 (9), e0256342. <https://doi.org/10.1371/journal.pone.0256342>.
- Desoky, E.M., Selem, E., El-Maati, M.F.A., Hassan, A.A.S.A., Belal, H.E.E., Rady, M.M., Al-Harbi, M.S., Ali, E.F., 2021. Foliar Supplementation of Clove Fruit Extract and Salicylic Acid Maintains the Performance and Antioxidant Defense System of *Solanum tuberosum* L. under Deficient Irrigation Regimes. *Horticulturae* 7 (11), 435. <https://doi.org/10.3390/horticulturae7110435>.
- Díaz-Pérez, J.C., Eaton, T.E., 2015. Eggplant (*Solanum melongena* L.) plant growth and fruit yield as affected by drip irrigation rate. *HortScience* 50 (11), 1709–1714. <https://doi.org/10.21273/hortsci.50.11.1709>.
- Echeverría-Londoño, S., Särkinen, T., Fenton, I.S., Purvis, A., Knapp, S., 2020. Dynamism and context-dependency in diversification of the megadiverse plant genus *Solanum* (Solanaceae). *J. Syst. Evol.* 58 (6), 767–782. <https://doi.org/10.1111/jse.12638>.
- Egea, I., Albaladejo, I., Meco, V., Morales, B., Sevilla, A., Bolarin, M.C., Flores, F.B., 2018. The drought-tolerant *Solanum pennellii* regulates leaf water loss and induces genes involved in amino acid and ethylene/jasmonate metabolism under dehydration. *Sci. Rep.* 8 (1) <https://doi.org/10.1038/s41598-018-21187-2>.
- Esan, V.I., Ayanbami, T., Omoyemi Adeyemo, J., Oluwafemi, S., 2018. Effect of Drought on Seed Germination and Early Seeding of Tomato Genotypes using Polyethylene Glycol 6000. *Int J 4* (02), 36–43. <https://doi.org/10.18483/ijsci.1533>.
- FAO. (2020.). Food and agriculture data. Available online at: <https://www.fao.org/faostat/en/#home>, Accessed date 23 January 2023.
- Fenstermaker, S., Cho, J., McCoy, J.E., Mercer, K.L., Francis, D.M., 2022. Selection strategies to introgress water deficit tolerance derived from *Solanum galapagense* accession LA1141 into cultivated tomato. *Front. Plant Sci.* 13, 947538 <https://doi.org/10.3389/fpls.2022.947538>.
- Fernandes, A., Chaski, C., Pereira, C., Kostic, M., Roupael, Y., Soković, M., Barros, L., Barros, L., 2022. Water stress alleviation effects of biostimulants on greenhouse-grown tomato fruit. *Horticulturae* 8 (7), 645. <https://doi.org/10.3390/horticulturae8070645>.
- Filiz, E., Akbudak, M.A., 2020. Ammonium transporter 1 (AMT1) gene family in tomato (*Solanum lycopersicum* L.): bioinformatics, physiological and expression analyses under drought and salt stresses. *Genomics* 112 (5), 3773–3782. <https://doi.org/10.1016/j.ygeno.2020.04.009>.
- Ford-Lloyd, B.V., Schmidt, M., Armstrong, S.J., Barazani, O., Engels, J., Hadas, R., Hammer, K., Kell, S.P., Kang, D., Khoshbakt, K., Li, Y., Long, C., Lu, B.R., Ma, K., Nguyen, V.T., Qiu, L., Ge, S., Wei, W., Zhang, Z., Maxted, N., 2011. Crop Wild Relatives—Undervalued, Underutilized and under Threat? *Bioscience* 61 (7), 559–565. <https://doi.org/10.1525/bio.2011.61.7.10>.
- Fu, Q.S., Yang, R.C., Wang, H.S., Zhao, B., Zhou, C.L., Ren, S.X., Guo, Y.D., 2013. Leaf morphological and ultrastructural performance of eggplant (*Solanum melongena* L.) in response to water stress. *Photosynthetica* 51 (1), 109–114. <https://doi.org/10.1007/s11099-013-0005-6>.
- Fullana-Pericás, M., Conesa, M.À., Gago, J., Ribas-Carbó, M., & Galmés, J. (2022). High-throughput phenotyping of a large tomato collection under water deficit: combining UAVs' remote sensing with conventional leaf-level physiologic and agronomic measurements. *Agricultural Water Management*, 260, 107283. <https://doi.org/10.1016/j.agwat.2021.107283>.
- Galdon-Armero, J., Fullana-Pericás, M., Mulet, P.A., Conesa, M.A., Martín, C., Galmés, J., 2018. The ratio of trichomes to stomata is associated with water use efficiency in *Solanum lycopersicum* (tomato). *Plant J* 96 (3), 607–619. <https://doi.org/10.1111/tplj.14055>.
- Galmés, J., Ochogavía, J.M., Gago, J., Roldán, E.J., Cifre, J., Conesa, M.N., 2013. Leaf responses to drought stress in Mediterranean accessions of *Solanum lycopersicum*: anatomical adaptations in relation to gas exchange parameters. *Plant Cell Environ.* 36 (5), 920–935. <https://doi.org/10.1111/pce.12022>.
- Goel, D., Singh, A.K., Yadav, V., Babbar, S.B., Bansal, K.C., 2010. Overexpression of osmotin gene confers tolerance to salt and drought stresses in transgenic tomato (*Solanum lycopersicum* L.). *Protoplasma* 245 (1–4), 133–141. <https://doi.org/10.1007/s00709-010-0158-0>.
- Gong, L., Zhang, H., Gan, X., Zhang, L., Chen, Y., Nie, F., Shi, L., Li, M., Guo, Z., Zhang, G., Song, Y., 2015. Transcriptome profiling of the potato (*Solanum tuberosum* L.) plant under drought stress and water-stimulus conditions. *PLoS ONE* 10 (5), e0128041. <https://doi.org/10.1371/journal.pone.0128041>.

- Gopal, J., Iwama, K., 2007. *In vitro* screening of potato against water-stress mediated through sorbitol and polyethylene glycol. *Cell Rep* 26 (5), 693–700. <https://doi.org/10.1007/s00299-006-0275-6>.
- Gramazio, P., Prohens, J., Plazas, M., Mangino, G., Herraiz, F.J., Vilanova, S., 2017. Development and genetic characterization of advanced backcross materials and an introgression line population of *Solanum incanum* in a *S. melongena* background. *Front. Plant Sci.* 8. <https://www.frontiersin.org/articles/10.3389/fpls.2017.01477>.
- Halford, N.G., Curtis, T.Y., Muttucumaru, N., Postles, J., Mottram, D.S., 2011. Sugars in crop plants. *Ann. Appl. Biol.* 158 (1), 1–25. <https://doi.org/10.1111/j.1744-7348.2010.00443.x>.
- Hill, D., Nelson, D., Hammond, J., Bell, L., 2021. Morphophysiology of Potato (*Solanum tuberosum*) in Response to Drought Stress: paving the Way Forward. *Front. Plant Sci.* 11, 597554 <https://doi.org/10.3389/fpls.2020.597554>.
- Hochberg, U., Herrera, J.C., Degu, A., Castellari, S.D., Peterlunger, E., Alberti, G., Lazarovitch, N., 2017. Evaporative demand determines the relative transpirational sensitivity of deficit-irrigated grapevines. *Irrigation Sci.* 35 (1), 1–9. <https://doi.org/10.1007/s00271-016-0518-4>.
- Hosseini Tafreshi, S.A., Aghaie, P., Ebrahimi, M.A., Haerinasab, M., 2021. Regulation of drought-related responses in tomato plants by two classes of calcineurin B-like (SLCBL1/2) proteins. *Plant Physiol Biochem* 162, 431–446. <https://doi.org/10.1016/j.plaphy.2021.03.014>.
- Huot, O.B., Tamborindeguy, C., 2017. Drought stress affects *Solanum lycopersicum* susceptibility to *B. actericaera* cockerelli colonization. *Entomol. Exp. Appl.* 165 (1), 70–82. <https://doi.org/10.1111/eea.12627>.
- Hwang, E.W., Shin, S.J., Yu, B.K., Byun, M.O., Kwon, H.B., 2011. miR171 family members are involved in drought response in *Solanum tuberosum*. *J. Plant Biol.* 54 (1), 43–48. <https://doi.org/10.1007/s12374-010-9141-8>.
- Ibañez, V.N., Kozub, P.C., González, C.V., Jerez, D.N., Masuelli, R.W., Berli, F.J., Marfil, C.F., 2021. Response to water deficit of semi-desert wild potato *Solanum kurtzianum* genotypes collected from different altitudes. *Plant Sci.* 308, 110911 <https://doi.org/10.1016/j.plantsci.2021.110911>.
- Imadi, S., Gul, A., Dikilitas, M., Karakas, S., Sharma, I., 2016. Water stress: types, causes, and impact on plant growth and development. In: Ahmad, P. (Ed.), *Water Stress and Crop Plants*. John Wiley & Sons, pp. 343–355. <https://doi.org/10.1002/9781119054450.ch21>.
- Jaarsma, R., de Vries, R.S.M., de Boer, A.H., 2013. Effect of salt stress on growth, na+ accumulation and proline metabolism in potato (*Solanum tuberosum*) Cultivars. *PLoS ONE* 8 (3), e60183. <https://doi.org/10.1371/journal.pone.0060183>.
- Kapoor, D., Bhardwaj, S., Landi, M., Sharma, A., Ramakrishnan, M., Sharma, A., 2020. The Impact of drought in plant metabolism: how to exploit tolerance mechanisms to increase crop production. *Appl. Sci.* 10 (16), 5692. <https://doi.org/10.3390/app10165692>.
- Kappachery, S., Yu, J.W., Baniekal-Hiremath, G., Park, S.W., 2013. Rapid identification of potential drought tolerance genes from *Solanum tuberosum* by using a yeast functional screening method. *C. R. Biol.* 336 (11–12), 530–545. <https://doi.org/10.1016/j.crvi.2013.09.006>.
- Karaca, P., Cekic, F.Z., 2019. Exogenous melatonin-stimulated defense responses in tomato plants treated with polyethylene glycol. *Int. J. Vegetable Sci.* 25 (6), 601–609. <https://doi.org/10.1080/19315260.2019.1575317>.
- Karkute, S.G., Gujjar, R.S., Rai, A., Akhtar, M., Singh, M., Singh, B., 2018. Genome wide expression analysis of WRKY genes in tomato (*Solanum lycopersicum*) under drought stress. *Plant Gene* 13, 8–17. <https://doi.org/10.1016/j.plgene.2017.11.002>.
- Kim, J., Kim, K.-S., Kim, Y., Chung, Y.S., 2020. A short review: comparisons of high-throughput phenotyping methods for detecting drought tolerance. *Sci. Agric.* 78. <https://doi.org/10.1590/1678-992X-2019-0300>.
- Korres, N.E., Norsworthy, J.K., Tehranchian, P., Gitsopoulos, T.K., Loka, D.A., Oosterhuis, D.M., Gealy, D.R., Moss, S.R., Burgos, N.R., Miller, M.R., Palhano, M., 2016. Cultivars to face climate change effects on crops and weeds: a review. *Agron. Sustainable Dev.* (1), 36. <https://doi.org/10.1007/s13593-016-0350-5>.
- Krishna, R., Ansari, W.A., Jaiswal, D.K., Singh, A.K., Verma, J.P., Singh, M., 2021. Co-overexpression of AtDREB1A and BcZAT12 increases drought tolerance and fruit production in double transgenic tomato (*Solanum lycopersicum*) plants. *Environ. Exp. Bot.* 184, 104396. <https://doi.org/10.1016/j.envexpbot.2021.104396>.
- Kulkarni, M., Deshpande, U., 2010. *In Vitro* screening of tomato genotypes for drought resistance using polyethylene glycol. *J. Biotechnol* 6 (ISSN: 1684-5315).
- Kulus, D., 2018. Genetic resources and selected conservation methods of tomato. *J. Appl. Botany Food Quality* 91 (2018). <https://doi.org/10.5073/JABFQ.2018.091.019>.
- Landi, S., Nurcato, R., de Lillo, A., Lentini, M., Grillo, S., Esposito, S., 2016. Glucose-6-phosphate dehydrogenase plays a central role in the response of tomato (*Solanum lycopersicum*) plants to short and long-term drought. *Plant Physiol. Biochem.* 105, 79–89. <https://doi.org/10.1016/j.plaphy.2016.04.013>.
- Leakey, A.D., Ferguson, J.N., Pignon, C.P., Wu, A., Jin, Z., Hammer, G.L., Lobell, D.B., 2019. Water use efficiency as a constraint and target for improving the resilience and productivity of C₃ and C₄ Crops. *Annu. Rev. Plant Biol.* 70 (1), 781–808. <https://doi.org/10.1146/annurev-arplant-042817-040305>.
- Lippman, Z.B., Semel, Y., Zamir, D., 2007. An integrated view of quantitative trait variation using tomato interspecific introgression lines. *Curr. Opin. Genet. Dev.* 17 (6), 545–552. <https://doi.org/10.1016/j.gde.2007.07.007>.
- Liu, Z., Coulter, J.A., Li, Y., Zhang, X., Meng, J., Zhang, J., Liu, Y., 2020. Genome-wide identification and analysis of the Q-type C2H2 gene family in potato (*Solanum tuberosum* L.). *Int. J. Biol. Macromol.* 153, 327–340. <https://doi.org/10.1016/j.ijbiomac.2020.03.022>.
- Machida-Hirano, R., Niino, T., 2017. Potato Genetic Resources. In: Kumar Chakrabarti, S., Xie, C., Tiwari, J.Kumar (Eds.), *The Potato Genome*. Springer International Publishing, pp. 11–30. https://doi.org/10.1007/978-3-319-66135-3_2.
- Mahalingam, R., 2015. Consideration of combined stress: a crucial paradigm for improving multiple stress tolerance in plants. In: Mahalingam, R. (Ed.), *Consideration of combined stress: a crucial paradigm for improving multiple stress tolerance in plants*. Combined Stresses in Plants: Physiol., Molecul. Biochem. Aspects 1–25. https://doi.org/10.1007/978-3-319-07899-1_1.
- Majeed, S., Chaudhary, M.T., Hulse-Kemp, A.M., Azhar, M.T., 2021. Chapter 1 - Introduction: crop Wild Relatives in Plant Breeding. In: Azhar, M.T., Wani, S.H. (Eds.), *Wild Germplasm for Genetic Improvement in Crop Plants*. Academic Press, pp. 1–18. <https://doi.org/10.1016/B978-0-12-822137-2.00001-1>.
- Martínez-Cuenca, M.R., Pereira-Dias, L., Soler, S., López-Serrano, L., Alonso, D., Calatayud, N., Díez, M.J., 2020. Adaptation to Water and Salt Stresses of *Solanum pimpinellifolium* and *Solanum lycopersicum* var. *cerasiforme*. *Agronomy* 10 (8), 1169. <https://doi.org/10.3390/agronomy10081169>.
- Matthews, S., Ali, A., Siddiqui, Y., Supramaniam, C.V., 2022. Plant Bio-stimulant: prospective, safe and natural resources. *J. Soil Sci. Plant Nutr.* 22 (2), 2570–2586. <https://doi.org/10.1007/s42729-022-00828-6>.
- Mattos, L.M., Moretti, C.L., 2016. Oxidative Stress in Plants Under Drought Conditions and the Role of Different Enzymes. *Enzyme Engineering* 5 (1). <https://doi.org/10.4172/2329-6674.1000136>.
- Meng, C., Yang, M., Wang, Y., Chen, C., Sui, N., Meng, Q., Zhuang, K., Lv, W., 2020. SIWHY2 interacts with SIRECA2 to maintain mitochondrial function under drought stress in tomato. *Plant Sci.* 301, 110674 <https://doi.org/10.1016/j.plantsci.2020.110674>.
- Mibeji, E.K., Ambuko, J., Giovannoni, J.J., Onyango, A.N., Owino, W.O., 2017. Carotenoid profiling of the leaves of selected African eggplant accessions subjected to drought stress. *Food Sci. Nutr.* 5 (1), 113–122. <https://doi.org/10.1002/fsn3.370>.
- Mishra, U., Rai, A., Kumar, R., Singh, M., Pandey, H.P., 2016. Gene expression analysis of *Solanum lycopersicum* and *Solanum habrochaites* under drought conditions. *Genom Data* 9, 40–41. <https://doi.org/10.1016/j.gdata.2016.04.001>.
- Morris, W., Taylor, M., 2017. The Solanaceous Vegetable Crops: potato, Tomato, Pepper, and Eggplant. *Encyclop. Appl. Plant Sci.* 55–58. <https://doi.org/10.1016/b978-0-12-394807-6.00129-5>.
- Nguyen, D., D'Agostino, N., Tytgat, T.O., Sun, P., Lortzing, T., Visser, E.J., Cristescu, S.M., Steppuhn, A., Mariani, C., Dam, N.M., Rieu, I., 2016. Drought and flooding have distinct effects on herbivore-induced responses and resistance in *Solanum dulcamara*. *Plant Cell Environ* 39 (7), 1485–1499. <https://doi.org/10.1111/pce.12708>.
- Nunes, C., Moreira, R., Pais, I., Semedo, J., Simões, F., Veloso, M.M., Scotti-Campos, P., 2022. Cowpea Physiological Responses to Terminal Drought—Comparison between Four Landraces and a Commercial Variety. *Plants* 11 (5), 593. <https://doi.org/10.3390/plants11050593>.
- Oladosu, Y., Rafii, M.Y., Arolo, F., Chukwu, S.C., Salisu, M.A., Olaniyan, B.A., Fagbohun, I.K., Muftaudeen, T.K., 2021. Genetic diversity and utilization of cultivated eggplant germplasm in varietal improvement. *Plants* 10 (8), 1714. <https://doi.org/10.3390/plants10081714>.
- Passioura, J.B., 2012. Phenotyping for drought tolerance in grain crops: when is it useful to breeders? *Funct. Plant Biol.* 39 (11), 851. <https://doi.org/10.1071/fp12079>.
- Per, T.S., Khan, N.A., Reddy, P.S., Masood, A., Hasanuzzaman, M., Khan, M.I.R., Anjum, N.A., 2017. Approaches in modulating proline metabolism in plants for salt and drought stress tolerance: phytohormones, mineral nutrients and transgenics. *Plant Physiol. Biochem.* 115, 126–140. <https://doi.org/10.1016/j.plaphy.2017.03.018>.
- Pereira, L.S., Allen, R.G., Smith, M., Raes, D., 2015. Crop evapotranspiration estimation with FAO56: past and future. *Agric. Water Manage.* 147, 4–20. <https://doi.org/10.1016/j.agwat.2014.07.031>.
- Pino, M.T.P., Ávila, A.R., Molina, A., Jeknic, Z., Chen, T.H., 2013. Enhanced *in vitro* drought tolerance of *Solanum tuberosum* and *Solanum commersonii* plants overexpressing the ScCBF1 gene. *Cienc. Invest. Agrar.* 40 (1), 171–184. <https://doi.org/10.4067/s0718-16202013000100015>.
- Plazas, M., González-Orenga, S., Nguyen, H.T., Morar, I.M., Fita, A., Boscaiu, M., Prohens, J., Vicente, O., 2022. Growth and antioxidant responses triggered by water stress in wild relatives of eggplant. *Sci. Hortic.* 293, 110685. <https://doi.org/10.1016/j.scienta.2021.110685>.
- Plazas, M., Nguyen, H.T., González-Orenga, S., Fita, A., Vicente, O., Prohens, J., Boscaiu, M., 2019. Comparative analysis of the responses to water stress in eggplant (*Solanum melongena*) cultivars. *Plant Physiol. Biochem.* 143, 72–82. <https://doi.org/10.1016/j.plaphy.2019.08.031>.
- Plazas, M., Vilanova, S., Gramazio, P., Rodríguez-Burruezo, A., Fita, A., Herraiz, F.J., Ranil, R., Fonseca, R., Niran, L., Fonseca, H., Kouassi, B., Kouassi, A., Kouassi, A., Prohens, J., 2016. Interspecific Hybridization between Eggplant and Wild Relatives from Different Genepools. *J. Am. Soc. Hortic. Sci.* 141 (1), 34–44. <https://doi.org/10.21273/jashs.141.1.34>.
- Pohl, A., Grabowska, A., Kalisz, A., Sekara, A., 2019. The eggplant yield and fruit composition as affected by genetic factor and biostimulant application. *Not. Bot. Horti. Agrobot. Cluj. Napoca* 47 (3). <https://doi.org/10.15835/nbha47311468>.
- Poudyal, D., Akash, M., Khatri, L., Shrestha, D.S., Uptmoor, R., 2017. *Solanum habrochaites* introgression line grafted as rootstock in cultivated tomato maintains growth and improves yield under cold and drought stresses. *J. Crop Improv.* 31 (4), 589–607. <https://doi.org/10.1080/15427528.2017.1319887>.
- Prashar, A., Yildiz, J., McNicol, J.W., Bryan, G.J., Jones, H.G., 2013. Infra-red thermography for high throughput field phenotyping in *Solanum tuberosum*. *PLoS ONE* 8 (6), e65816. <https://doi.org/10.1371/journal.pone.0065816>.
- Rady, M.M., Belal, H.E., Gadallah, F.M., Semida, W.M., 2020. Selenium application in two methods promotes drought tolerance in *Solanum lycopersicum* plant by inducing the antioxidant defense system. *Sci. Hortic.* 266, 109290. <https://doi.org/10.1016/j.scienta.2020.109290>.

- Reynolds, M., Chapman, S., Crespo-Herrera, L., Molero, G., Mondal, S., Pequeno, D.N., Pinto, F., Pinera-Chavez, F.J., Poland, J., Rivera-Amado, C., Saint Pierre, C., Sukumaran, S., 2020. Breeder friendly phenotyping. *Plant Sci.* 295, 110396 <https://doi.org/10.1016/j.plantsci.2019.110396>.
- Robertson, B.B., Carrick, S.T., Almond, P.C., McNeill, S., Penny, V., Chau, H.W., Smith, C. M., 2021. Predicting field capacity in undisturbed stony soils. *Geoderma* 401, 115346. <https://doi.org/10.1016/j.geoderma.2021.115346>.
- Rolando, J.L., Ramírez, D.A., Yactayo, W., Monneveux, P., Quiroz, R., 2015. Leaf greenness as a drought tolerance related trait in potato (*Solanum tuberosum* L.). *Environ. Exp. Bot.* 110, 27–35. <https://doi.org/10.1016/j.envexpbot.2014.09.006>.
- Sakya, A.T., Sulistyaningsih, E., Indradewa, D., & Purwanto, B.H. (2018). Physiological characters and tomato yield under drought stress. *IOP Conference Series: Earth and Environmental Science*, 200, 012043. [10.1088/1755-1315/200/1/012043](https://doi.org/10.1088/1755-1315/200/1/012043).
- Schafleitner, R., Gutierrez, R., Espino, R., Gaudin, A., Pérez, J., Martínez, M., Domínguez, A., Tincopa, L., Alvarado, C., Numberto, G., Bonierbale, M., 2007. Field Screening for Variation of Drought Tolerance in *Solanum tuberosum* L. by Agronomical, Physiological and Genetic Analysis. *Potato Res.* 50 (1), 71–85. <https://doi.org/10.1007/s11540-007-9030-9>.
- Schreinemachers, P., Simmons, E.B., Wopereis, M.C., 2018. Tapping the economic and nutritional power of vegetables. *Glob. Food Sec.* 16, 36–45. <https://doi.org/10.1016/j.gfs.2017.09.005>.
- Semida, W.M., Abdelkhalik, A., Mohamed, G.F., Abd El-Mageed, T.A., Abd El-Mageed, S. A., Rady, M.M., Ali, E.F., 2021. Foliar application of zinc oxide nanoparticles promotes drought stress tolerance in eggplant (*Solanum melongena* L.). *Plants* 10 (2), 421. <https://doi.org/10.3390/plants10020421>.
- Siaga, E., Maharijaya, A., Rahayu, M.S., 2016. Plant growth of eggplant (*Solanum melongena* L.) *in vitro* in drought stress polyethylene glycol (PEG). *Biol. Res.* 2 (1) <https://doi.org/10.24233/biov.2.1.2016.29>.
- Singh, A., Ganapathysubramanian, B., Singh, A.K., Sarkar, S., 2016. Machine learning for high-throughput stress phenotyping in plants. *Trends Plant Sci.* 21 (2), 110–124. <https://doi.org/10.1016/j.tplants.2015.10.015>.
- Slama, I., Abdelly, C., Bouchereau, A., Flowers, T., Savouré, A., 2015. Diversity, distribution and roles of osmoprotective compounds accumulated in halophytes under abiotic stress. *Ann. Bot.* 115 (3), 433–447. <https://doi.org/10.1093/aob/mcu239>.
- Solh, M., van Ginkel, M., 2014. Drought preparedness and drought mitigation in the developing world's drylands. *Weather Clim Extrem* 3, 62–66. <https://doi.org/10.1016/j.wace.2014.03.003>.
- Sseremba, G., Tongoon, P., Eleblu, J., Danquah, E.Y., Kizito, E.B., 2018. Heritability of drought resistance in *Solanum aethiopicum* Shum group and combining ability of genotypes for drought tolerance and recovery. *Sci. Hortic.* 240, 213–220. <https://doi.org/10.1016/j.scienta.2018.06.028>.
- Sudiro, C., Guglielmi, F., Hochart, M., Senizza, B., Zhang, L., Lucini, L., Altissimo, A., 2022. A Phenomics and Metabolomics Investigation on the Modulation of Drought Stress by a Biotstimulant Plant Extract in Tomato (*Solanum lycopersicum*). *Agronomy* 12 (4), 764. <https://doi.org/10.3390/agronomy12040764>.
- Szalonek, M., Sierpien, B., Rymaszewski, W., Gieczewska, K., Garstka, M., Lichocka, M., Sass, L., Paul, K., Vass, I., Vankova, R., Dobrev, P., Szczesny, P., Marczewski, W., Krusiewicz, D., Strzelczyk-Zyta, D., Hennig, J., Konopka-Postupolska, D., 2015. Potato Annexin STANN1 Promotes Drought Tolerance and Mitigates Light Stress in Transgenic *Solanum tuberosum* L. *Plants*. *PLoS ONE* 10 (7), e0132683. <https://doi.org/10.1371/journal.pone.0132683>.
- Takács, S., Pék, Z., Csányi, D., Daoud, H.G., Szuvandzsev, P., Palotás, G., Helyes, L., 2020. Influence of Water Stress Levels on the Yield and Lycopene Content of Tomato. *Water (Basel)* 12 (8), 2165. <https://doi.org/10.3390/w12082165>.
- Tamburino, R., Vitale, M., Ruggiero, A., Sassi, M., Sannino, L., Arena, S., Costa, A., Batelli, G., Zambrano, N., Scaloni, A., Grillo, S., Scotti, N., 2017. Chloroplast proteome response to drought stress and recovery in tomato (*Solanum lycopersicum* L.). *BMC Plant Biol.* 17 (1) <https://doi.org/10.1186/s12870-017-0971-0>.
- Tang, Z., Jin, Y., Brown, P.H., Park, M., 2023. Estimation of tomato water status with photochemical reflectance index and machine learning: assessment from proximal sensors and UAV imagery. *Front Plant Sci* 14. <https://www.frontiersin.org/articles/10.3389/fpls.2023.1057733>.
- Tani, E., Kizis, D., Markellou, E., Papadakis, I., Tsamadia, D., Leventis, G., Makrogianni, D., Karapanos, I., 2018. Cultivar-Dependent Responses of Eggplant (*Solanum melongena* L.) to Simultaneous Verticillium dahliae Infection and Drought. *Front Plant Sci* 9, 1181. <https://doi.org/10.3389/fpls.2018.01181>.
- Tapia, G., Méndez, J., Inostroza, L., 2016. Different combinations of morpho-physiological traits are responsible for tolerance to drought in wild tomatoes *Solanum chilense* and *Solanum peruvianum*. *Plant Biol.* 18 (3), 406–416. <https://doi.org/10.1111/plb.12409>.
- Teshome, D.T., Zharare, G.E., Naidoo, S., 2020. The Threat of the Combined Effect of Biotic and Abiotic Stress Factors in Forestry Under a Changing Climate. *Front Plant Sci* 11, 601009. <https://doi.org/10.3389/fpls.2020.601009>.
- Top, S., Vandoorne, B., Pauwels, E., Perneel, M., Van Labeke, M., Steppe, K., 2023. Plant Sensors Untangle the Water-Use and Growth Effects of Selected Seaweed-Derived Biostimulants on Drought-Stressed Tomato Plants (*Solanum lycopersicum*). *J. Plant Growth Regul.* <https://doi.org/10.1007/s00344-023-10941-0>.
- Uddin, M.N., Hossain, M.A., Burritt, D.J., 2016. Salinity and drought: similarities and differences in oxidative responses and cellular redox regulation. In: Ahmad, P. (Ed.), *Water Stress and Crop Plants*. John Wiley & Sons, Ltd., pp. 86–101. <https://doi.org/10.1002/9781119054450.ch7>.
- Veihmeyer, F.J., Hendricksom, A.H., 1931. The moisture equivalent as a measure of the field capacity of soils. *Soil Sci* 32 (3), 181–194. <https://doi.org/10.1097/00010694-193109000-00003>.
- Villanueva, G., Vilanova, S., Plazas, M., Prohens, J., Gramazio, P., 2023. Transcriptome profiles of eggplant (*Solanum melongena*) and its wild relative *S. dasyphyllum* under different levels of osmotic stress provide insights into response mechanisms to drought. *Current Plant Biology* 33, 100276. <https://doi.org/10.1016/j.cpb.2023.100276>.
- Waseem, M., Rong, X., Li, Z., 2019. Dissecting the Role of a Basic Helix-Loop-Helix Transcription Factor, SlbHLH22, Under Salt and Drought Stresses in Transgenic *Solanum lycopersicum* L. *Front Plant Sci* 10, 734. <https://doi.org/10.3389/fpls.2019.00734>.
- Wu, Q., Hu, Y., Sprague, S.A., Kakeshpour, T., Park, J., Nakata, P.A., Cheng, N., Hirschi, K.D., White, F.F., Park, S., 2017. Expression of a monothiol glutaredoxin, AtGRXS17, in tomato (*Solanum lycopersicum*) enhances drought tolerance. *Biochem. Biophys. Res. Commun.* 491 (4), 1034–1039. <https://doi.org/10.1016/j.bbrc.2017.08.006>.
- Yavuz, D., Seymen, M., Yavuz, N., Çoklar, H., Ercan, M., 2021. Effects of water stress applied at various phenological stages on yield, quality, and water use efficiency of melon. *Agric. Water Manage.* 246, 106673. <https://doi.org/10.1016/j.agwat.2020.106673>.
- Zacharias, S., Bohne, K., 2008. Attempt of a flux-based evaluation of field capacity. *J. Plant Nutr. Soil Sci.* 171 (3), 399–408. <https://doi.org/10.1002/jpln.200625168>.
- Zayova, E., Philipov, P., Nedev, T., Stoeva, D., 2017. Response of *in vitro* cultivated eggplant (*Solanum melongena* L.) to salt and drought stress. *AgroLife Scientific Journal* 6 (1), 276–282. <https://www.cabdirect.org/cabdirect/abstract/20173216408>.
- Zhang, F., Shi, Y., Ali, J., Xu, J., Li, Z., 2021. Breeding by selective introgression: theory, practices, and lessons learned from rice. *Crop J.* 9 (3), 646–657. <https://doi.org/10.1016/j.cj.2021.03.006>.
- Zhu, M., Chen, G., Zhang, J., Zhang, Y., Xie, Q., Zhao, Z., Pan, Y., Hu, Z., 2014. The abiotic stress-responsive NAC-type transcription factor SlNAC4 regulates salt and drought tolerance and stress-related genes in tomato (*Solanum lycopersicum*). *Cell Rep.* 33 (11), 1851–1863. <https://doi.org/10.1007/s00299-014-1662-z>.