

KONYA FOOD AND AGRICULTURE UNIVERSITY
GRADUATE SCHOOL
DEPARTMENT OF PLANT PRODUCTION AND
TECHNOLOGIES

THE EFFECTS OF NaCl-SEED PRIMING AND PLANT
GROWTH PROMOTING BACTERIA (PGPB)
APPLICATIONS ON THE PHYSIOLOGICAL RESPONSES
OF A SALT SENSITIVE MELON VARIETY TO SALT
STRESS

MASTER OF SCIENCE THESIS

Hüsna DOLU

KONYA
JUNE, 2024

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TO SALT STRESS**

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ABSTRACT

THE EFFECTS OF NaCl-SEED PRIMING AND PLANT GROWTH PROMOTING BACTERIA (PGPB) APPLICATIONS ON THE PHYSIOLOGICAL RESPONSES OF A SALT SENSITIVE MELON VARIETY TO SALT STRESS

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Master of Science Thesis, Department of Plant Production & Technologies

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Soil salinization poses a significant threat to the environment and food security, with nearly 1 billion hectares of land globally classified as 'saline.' Given the varying salt tolerance of plants at different growth stages, particularly during germination, combined salt stress alleviation techniques are essential. This study examines the individual and combined effects of NaCl-seed priming and Plant Growth Promoting Bacteria (PGPB) inoculation on melon plants to mitigate salinity effects, using a 150 mM NaCl solution for irrigation over 22 days. Under stress conditions, the P group exhibited superior seed germination, with a 15.5% increase in total germination rate. The research found that salt stress severely reduces the photosynthetic efficiency of melon plants, indicated by declines in maximum fluorescence (F_m), quantum efficiency (Φ_{PSII}), and performance index (PI_{ABS}) in long-term. While seed priming and PGPB treatments provided some protective benefits, their combined application under salt stress often resulted in negative interactions, diminishing overall effectiveness. Therefore, the optimal use of these treatments requires careful consideration of specific plant species and stress conditions to enhance stress tolerance.

Keywords: Soil Salinization, Seed Priming, Plant Growth Promoting Bacteria (PGPB), Salt Stress, Melon (*Cucumis melo* L.)

ÖZET

TOHUMDA NaCl-PRIMING İŞLEMİNİN VE BİTKİ BÜYÜMESİNİ DESTEKLEYEN BAKTERİ (PGPB) UYGULAMALARININ, TUZ STRESİ ALTINDA, TUZ STRESİNE HASSAS KAVUN ÇEŞİDİNİN FİZYOLOJİK TEPKİLERİ

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Toprak tuzluluğu, yaklaşık 1 milyar hektar arazinin 'tuzlu' olarak sınıflandırılmasıyla, çevreyi ve gıda güvenliğini önemli ölçüde tehdit etmektedir. Bitkilerin farklı büyüme aşamalarındaki, özellikle çimlenme dönemindeki, değişen tuz toleransı göz önüne alındığında, kombine tuz stresi hafifletme teknikleri esastır. Bu çalışma, NaCl tohum priming ve Bitki Büyümesini Teşvik Eden Bakteri (PGPB) inokülasyonunun kavun bitkileri üzerindeki bireysel ve kombine etkilerini inceleyerek tuzluluğun etkilerini hafifletmeyi amaçlamaktadır ve 22 gün boyunca her iki günde bir 150 mM NaCl çözeltisi kullanılarak sulama yapılmıştır. Stres koşulları altında, P grubu, toplam çimlenme oranında %15,5'lik bir artışla üstün bir tohum çimlenme sergilemiştir. Araştırma, tuz stresinin kavun bitkilerinin fotosentetik verimliliğini önemli ölçüde azalttığını, maksimum floresan (Fm), PSII kuantum verimliliği (ΦPSII) ve performans indeksi (PI_{ABS}) değerlerinde uzun vadede düşüşlerle gösterdiğini bulmuştur. Tohum priming ve PGPB uygulamaları bazı koruyucu faydalar sağlarken, tuz stresi altında bu tedavilerin kombinasyonu genellikle olumsuz etkileşimlere yol açarak genel etkinliği azaltmıştır. Bu nedenle, bu yöntemlerin optimal kullanımı, stres toleransını artırmak için belirli bitki türleri ve stres koşullarının dikkatli bir şekilde değerlendirilmesini gerektirmektedir.

Anahtar Kelimeler: Toprak Tuzluluğu, Tohum Priming, Bitki Büyüme Destekleyici Bakteri (PGPB), Tuz Stresi, Kavun (*Cucumis melo* L.)

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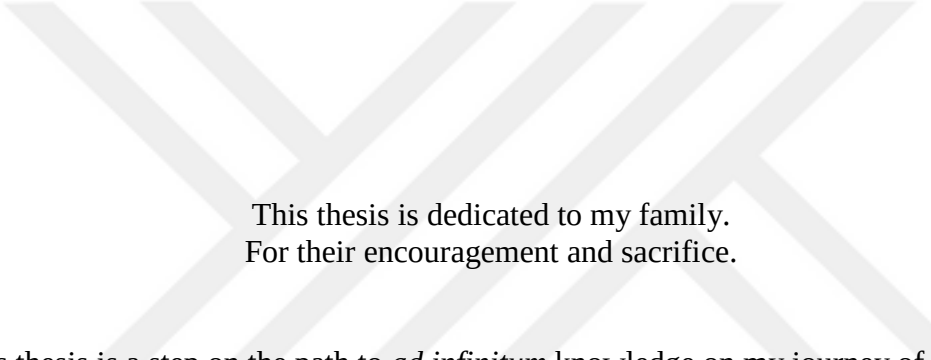
On a personal level, I owe a debt of gratitude to my family - my mother M*****e D**U, father E*****n D**U, and sister F***a N*r D**U. Their unwavering emotional and financial support have been the backbone of my achievements.

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H***a D**U
June-2024

DEDICATION



This thesis is dedicated to my family.
For their encouragement and sacrifice.

This thesis is a step on the path to *ad infinitum* knowledge on my journey of lifelong learning.

If all the trees on earth were pens and the ocean 'were ink', refilled by seven other oceans, the Words of Allah would not be exhausted. Surely Allah is Almighty, All-Wise.
(Surah Luqman, Verse 2)

TEXT OF OATH

The study I presented as my Master of Science thesis titled “The Effects of NaCl-Seed Priming and Plant Growth Promoting Bacteria (PGPB) Applications on the Physiological Responses of a Salt Sensitive Melon Variety to Salt Stress” has been written without applying to any assistance inconsistent with the scientific ethics and traditions, and all sources I have benefited from were listed in bibliography and I have been used them by means of making references and I declare and confirm this with my honor.

28/06/2024

H***a D**U

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LIST OF SYMBOLS AND ABBREVIATIONS

Symbols

°C	Celcius degree
ABS/RC	Absorption efficiency per reaction center
dS	Decisiemens
EC	Electrical Conductivity
ETo/RC	Electron transport rate beyond plastoquinone-A
Fm	Maximum fluorescence
ms	Milliseconds
Fo	Minimum fluorescence yield
PI _{ABS}	Performance index based on light absorption
ΦPo, Fv/Fm	Potential for primary photochemistry

Abbreviations

P680	A reaction center chlorophyll dimer
ABA	Abscisic acid
AMF	Arbuscular mycorrhizal fungi
APX	Ascorbate peroxidase
CAT	Catalase
Chl a	Chlorophyll a
DAS	Days after salt stres
FAO	Food and Agriculture Organization
GPX	Glutathione peroxidase
GR	Glutathione reductase
LHCII	Light-harvesting antenna complex
OM	Organic matter
OEC	Oxygen-evolving complex
Pheo	Pheophytin
PSI	Photosystem I
PSII	Photosystem II
PQH ₂	Plastohydroquinone
PQ	Plastoquinone
RC	Reaction centers
ROS	Reactive oxygen species
SOD	Superoxide dismutase
WWF	The World Wide Fund for Nature
TÜİK	Turkish Statistical Institute

1. INTRODUCTION

1.1. Soil Salinity

Agricultural lands in arid and semi-arid regions faced increasing soil salinity during recent years. Elevated salinity levels in irrigation water exacerbates the problem of soil salinization, leading to a series of adverse outcomes. According to the FAO (the Food and Agriculture Organization), over 833 million hectares of the World's soil were classified as "saline" by 2021, with more than 10% of cropland facing this issue (FAO, 2021b; Squires & Glenn, 2004). This translates to a significant portion of agricultural land. Mapping studies, however, including a recent study by Negacz, Malek, de Vos, & Vellinga (2022) estimate a much larger area, with a total saline soil area reaching approximately 1.7 billion hectares worldwide. These studies have shown an increasing trend in soil salinity over the years, with the greatest increase occurring in partially saline areas (Ivushkin *et al.*, 2019). This indicates that even areas not yet affected by salt are at high risk, and necessary measures should be taken sooner rather than later. High salt concentration in the soil increases osmotic pressure, preventing plants from taking up water and causing drought stress (Russo, 2023). Furthermore, salts, such as NaCl, can have toxic effects on plant physiology (Schmöckel & Jarvis, 2017). This poses a major threat to global food security.

Soil salinization occurs due to the accumulation of salt-forming ions, namely K^+ , Na^+ , Mg^{+2} , Ca^{+2} , Cl^- , SO_4^{-4} , CO_3^{-3} , and HCO_3^- in the soil (Singh, 2021). Soil salinity, is conventionally measured as the electrical conductivity of a saturated paste at 25 °C (ECe, dS/m), harms sensitive crops above 2 dS/m. Salt-tolerant varieties and improved soil management may alleviate the problem, but most crops struggle at 4 dS/m or higher (Abrol, Yadav, & Massoud, 1988). The aforementioned study identified a concerning trend, with over 200 million hectares exceeding this critical threshold (Negacz *et al.*, 2022). It is worth noting that accumulating sodium cations is specifically referred to as sodification. Soil sodicity significantly impacts soil structure by elevating soil pH and restricting Ca^{+2} uptake (Wiesman, 2009).

Soil salinization and sodification can arise from inherent factors like soil structure and groundwater properties (primary salinization) or from human activities related to land management (secondary salinization). The characteristics of the land, such as parent rock,

topography, climate, vegetation, and groundwater infiltration, all play a role in primary salinization (Okur & Örçen, 2020). For instance, high water table contributes to salinization of the topsoil, because the evaporation of readily available groundwater leads to the concentration of solutes on the surface (Rengasamy, 2006). Coastal areas are also susceptible to salinization due to saltwater intrusion, as exemplified by the situation along half of Bangladesh's coastline (Haque, 2006). However, agricultural practices can significantly influence salinization. Excessive irrigation, poor drainage, use of low-quality water, deep tillage, destruction of natural vegetation, over-extraction of groundwater, and excessive use of fertilizers and pesticides can all contribute to secondary salinization, particularly in intensive farming focused on short-term gains (Okur & Örçen, 2020). In regions with high evaporation rates, saline minerals often accumulate on the soil surface when poorly drained soils are irrigated with low-quality water (Allison, 1964). A recent nine-year study conducted on a vineyard irrigated with reclaimed wastewater revealed that nearly one-third of the vines stunted or withered due to the sodium accumulation in the soil (Simhayov, Ohana-Levi, Shenker, & Netzer, 2023). Australia exemplifies salinization caused by modifications to its natural vegetation cover. The replacement of Australia's perennial local flora with annual crops disrupts the soil water equilibrium. This disruption leads to waterlogging and the upward movement of brackish groundwater closer to the surface (Clarke, George, Bell, & Hatton, 2002).

1.2. Soil Salinity in Türkiye

Approximately 27% of Türkiye's 24 million ha of crop production area practices irrigation-based agriculture (Kalkınma Bakanlığı, 2018; TÜİK, 2022a). The Konya closed basin, which accounts for 10% of this area with 2.2 million ha, significantly contributes to the country's agricultural production (TÜİK, 2022b). Due to the region's semi-arid climate, high ground water, and low slope, irrigated agriculture makes it prone to salinity and sodicity problems (WWF, 2014). According to the Turkish Ministry of Forestry and Water Affairs (2015), 40,000 hectares of soil in the basin are composed of saline-alkali and saline-alkali mixed soils that are unsuitable for cultivation.

1.3. Melon

Melon (*Cucumis melo* L.) is a member of the genus *Cucumis* in the family *Cucurbitaceae*, with another prominent member, cucumber (*C. sativus* L.). Global production reached an

estimated 29 million tons in 2021, with China leading as the primary producer (14 million tons), followed by Türkiye, India, Kazakhstan, and Afghanistan (FAO, 2021a). Melon cultivation primarily targets its fruit, which is harvestable at various stages of ripeness. Known for their abundance of sucrose, melons are typically eaten fresh, although cooking and pickling are alternative methods of consumption (Pitrat, 2008).

According to FAO (2021a), Türkiye is the second-largest producer of melons after China. Beyond being a global producer, Türkiye also serves as a secondary region promoting the diversification of melon genes, encompassing populations distributed across a vast region, extending from South Asia to Japan (Pitrat, Chauvet, & Foury, 1999). Local Turkish melon accessions exhibit a remarkably high degree of diversity (Sari & Solmaz, 2007; Sari *et al.*, 2008; Sensoy, Büyükalaca, & Abak, 2007). Notably, melons belonging to the *Cantalupensis* group are believed to have originated in eastern Türkiye and subsequently spread westward into Europe (Szamosi, Solmaz, Sari, & Bársony, 2010).

Melons are classified as partially tolerant to salt (Akrami & Arzani, 2019) and are typically grown in high-salinity soils in Türkiye and around the world (Franco, Fernández, Bañón, & González, 1997). This can lead to issues such as reduced yield and morphological disorders. Various studies have determined the salt tolerance threshold of melon to be 1.11 dS/m (Mangal, Hooda, & Lal, 1988), 1.73 dS/m (Tedeschi, Lavini, Riccardi, Pulvento, & d'Andria, 2011), and 2.7 dS/m (Huang *et al.*, 2012). In Konya, which is the second-largest melon producer in Türkiye, 39% of soils have EC values above 2 dS/m (Taş, Yıldırım, Özkay, & Aras, 2013). In the region, particularly in Çumra district, salinity levels increase due to irrigation, which is influenced by climate and soil characteristics (Taş *et al.*, 2013; TÜİK, 2022b). According to Bahçeci *et al.* (2006), salinity in the Çumra region was measured at 2.7 dS/m.

1.4. Effects of Soil Salinity

One billion hectares of the world's agricultural land are classified as 'saline' (FAO, 2021b; Squires & Glenn, 2004). This widespread soil-based abiotic stress threatens the socioeconomic structures, global food security, and environment.

1.4.1. Socioeconomic Effects

Farmers facing soil salinization often resort to increased use of synthetic fertilizers to maintain crop yields. Although these fertilizers temporarily promote plant growth, their

long-term use can exacerbate salinization and ecosystem disruption (Adesemoye & Kloepper, 2009; Lazcano, Gómez-Brandón, Revilla, & Domínguez, 2013). This creates a vicious cycle of requiring more fertilizer to ensure productivity at an ever-increasing economic burden. The economic pressure resulting from these challenges can force farming families to abandon their fields due to financial constraints. This, in turn, causes rural communities to migrate to metropolitan areas in search of opportunity, resulting in urban overpopulation. These changes have a profound impact on communities, leading to food shortages, increased hunger, and higher levels of poverty (Salvati & Ferrara, 2015).

1.4.2. Effects on Food Security

Financial constraints, displacement, deterioration of once-fertile lands, and reduced crop quality caused by soil salinization ultimately jeopardize global food security. Feeding the growing global population becomes increasingly strained as a result. Crop yield losses in salt-affected areas stem from the detrimental effects of salt stress on plants at the cellular level. When exposed to salt stress, plants occlude stomatal aperture to limit transpiration, thereby curtailing the CO₂ availability to the leaves. This, in turn, disrupts the photosynthetic electron transport chain, downregulating photosynthesis and generating the oxygen free radicals (Muhammad Ashraf & Akram, 2009; Thompson, Legge, & Barber, 1987). Reactive Oxygen Species (ROS, e.g. hydrogen peroxide, superoxide anion, and singlet oxygen) induce toxic conditions in the cytoplasm (Ahsan, Ali, & Ali, 2003; Mckersie & Leshem, 1994). In fact, ROS are byproducts of metabolic activities in the mitochondria and cytoplasm, even under non-stress conditions, and contribute to cellular communication and signaling pathways (Dat *et al.*, 2003, 2000; Laloi, Apel, & Danon, 2004). Cells produce various enzymatic and non-enzymatic compounds to detoxify the ROS, called antioxidants (Asada, 1999). However, when this scavenging response becomes overwhelmed due to abiotic or biotic stresses, ROS distort cell metabolism through oxidation of cell constituents such as phospholipid bilayers, functional proteins, and DNA/RNA (Mckersie & Leshem, 1994). These cellular disruptions ultimately translate into the observed consequences at the field level, such as reduced nutritional value, stunted growth, and toxicity in crops. This interconnected relationship underscores the profound threat soil salinity poses not only to the environment but also to global food security (Lamz Piedra & González Cepero, 2013).

1.4.3. Environmental Effects

The decline in agricultural output due to soil salinity ultimately stems from the environmental impact of salt on the soil itself. Examination of the environmental impacts of soil salinity reveals a cascade of detrimental effects, including the extinction of salt-sensitive plants and soil-dwelling organisms due to excessive soluble salt levels (Bui, 2013). This selective pressure allows adapted, salt-tolerant organisms to dominate, further contributing to the degradation of soil structure and quality. Consequently, once-diverse ecosystems are transformed into barren, desert-like landscapes (Corwin, 2021). Furthermore, the soil microbial community, a cornerstone of nutrient cycling, is also susceptible to disruption by these transformations (Zhang, Wang, Xue, & Wang, 2019). This disruption manifests as a reduction in several soil biogeochemical outputs, including microbial biomass and activity, enzymatic decomposition, and overall respiratory rates – all crucial indicators of ecosystem dysfunction (Rath & Rousk, 2015; Tripathi *et al.*, 2006). Notably, Rousk, Elyaagubi, Jones, & Godbold (2011) found a clear negative correlation between salinity and bacterial proliferation. The study further investigates the ameliorative potential of organic matter (OM) content on the soil microbiome by introducing a coconut-based carbon source under salt stress. Thriving soil microbial communities play a critical role in all aspects of nutrient cycling, including OM decomposition, soil stability, and maintenance of pore space, all of which directly affect nutrient availability to plants (Marschner, 2011). Therefore, the effects of salt on microbial processes can significantly reduce soil OM content and nutrient availability, ultimately leading to reduced fertility in saline soils (Setia *et al.*, 2012). A recent study by (Zhang *et al.*, 2019) reported that the population size of soil microorganisms varied in response to salinity. While beneficial bacteria crucial for OM incorporation and fixation declined, fungal taxa potentially linked to accelerated OM breakdown thrived as salinity levels rose. Additionally, high salinity reduced the abundance of arbuscular mycorrhizal fungal strains, essential for plant P and K uptake and for maintaining healthy OM quality. These observed changes in microbial community composition, alongside documented reductions in soil OM content, microbial biomass, and available K, collectively suggest a significant negative impact of salinity on soil fertility, likely mediated through alterations in the soil microbiome.

In conclusion, soil salinity presents a multifaceted challenge, jeopardizing agricultural output, global food security, and the health of soil ecosystems. While increased fertilizer application is acknowledged as a solution for crop yields, it poses a threat to the financial viability of agricultural practices and the sustainability of environmental resources, particularly soil and groundwater quality (Zhu, Li, Christie, & Li, 2005). A sustainable approach is imperative to address the main causes of soil salinity and restore the delicate balance within the soil. This approach should focus on fostering beneficial biological interactions and promoting natural mechanisms for mitigating stress and maintaining soil health.

1.5. Plant Responses to Salt Stress

Plants exhibit various biochemical responses to counter the environmental challenges posed by soil salinization.

1. **Ion Regulation and Cellular Organization:** Plants work to maintain ion homeostasis by regulating the uptake and sequestration of ions like sodium (Na^+) and potassium (K^+) (Niu, Bressan, Hasegawa, & Pardo, 1995).
2. **Biosynthesis of Osmotic Regulators:** Organic osmolytes such as sugars, polyols, proline, and glycine betaine helps maintain cellular osmotic balance, preventing dehydration (Ahmad, Jaleel, Salem, Nabi, & Sharma, 2010; Muhammad Ashraf & Foolad, 2007).
3. **Antioxidant Enzyme Activation:** Activation of antioxidant enzymes such as catalase (CAT), glutathione reductase (GR), ascorbate peroxidase (APX), superoxide dismutase (SOD), and glutathione peroxidase (GPX) counteracts salt-induced oxidative stress (Groß, Durner, & Gaupels, 2013).
4. **Polyamine Synthesis and Regulation:** Polyamines, such as spermine and spermidine, are synthesized to protect cell membranes and proteins, aiding in stress tolerance (K. Gupta, Dey, & Gupta, 2013).
5. **Nitric Oxide (NO) Generation and Modulation:** Nitric oxide functions as a signal transducing compound involved in several stress pathways, including salt stress, in plants (Shi *et al.*, 2012).
6. **Hormonal Regulation and Signaling:** Salt stress induces changes in hormone levels, particularly abscisic acid (ABA) and ethylene, to trigger adaptive

responses and signaling pathways to stress (He & Cramer, 1996; Tao *et al.*, 2015).

Together, these responses contribute to a plant's resilience to salt stress and the maintenance of cellular functions (B. Gupta & Huang, 2014).

Plants manage absorbed light energy through three competing pathways: photosynthesis, thermal dissipation, and chlorophyll fluorescence (Maxwell & Johnson, 2000). Under environmental stress, plants often prioritize thermal dissipation, releasing excess energy as heat. This shift in energy flow is detectable through the OJIP chlorophyll fluorescence transient, a versatile tool for monitoring plant responses to stresses like salt (Schreiber, Bilger, & Neubauer, 1995).

1.6. Strategies to Mitigate Soil Salinity

The increasing concern regarding global soil salinization and sodicity requires the development of effective strategies to ensure food security. These strategies can be broadly categorized into two approaches: soil rehabilitation and enhancing plant tolerance to salinity.

A diverse range of soil remediation techniques is available, with leaching being the most widely practiced, facilitates the removal of salts. However, it can potentially disrupt soil biochemistry and necessitate significant water resources, which are often scarce in arid regions (Shankar & Evelin, 2019; Shaygan & Baumgartl, 2022). Incorporating organic soil amendments can enhance the performance of leaching in arid environments (Mahmoodabadi, Yazdanpanah, Sinobas, Pazira, & Neshat, 2013). In the cases of soil compaction and surface salinity, ripping and scraping can be implemented to physically remove salt from the soil (Bradshaw, 1997; Le Houérou, 1992; Shaygan, Mulligan, & Baumgartl, 2018).

Cultivation of halophytes (i.e., salt-resistant plants) offers a sustainable approach in saline lands known as phytoremediation, or specifically phytodesalinization (Manousaki & Kalogerakis, 2011; Rabhi *et al.*, 2010). Halophytes harbor various mechanisms to endure salinity, including the accumulation of salts within their tissues and excretion through specialized glands (i.e., salt glands) (Dassanayake & Larkin, 2017). This method proves to be both cost-effective and environmentally friendly, albeit requiring considerable time. Subsequent to harvest, the roots of these plants contribute to enhanced soil aeration and

water infiltration by creating pores. Moreover, the harvested halophyte biomass may hold potential as fodder. The *Chenopodioideae* family, *Suaeda* spp., *Salicornia* spp., and *Atriplex* spp., harbors a multitude of well-adapted halophytes (Shaygan & Baumgartl, 2022; Ventura & Sagi, 2013).

It is important to recognize that even with the utilization of halophytes, leaching may still be indispensable in arid climates to attain optimal soil amelioration. Overall, soil rehabilitation approaches frequently entail significant costs and may yield short-lived results, particularly when managing with variable salinity levels across a field (Shannon & Qualset, 1984).

The increasing prevalence of salinized agricultural land necessitates alternative solutions to complete abandonment or resource-intensive reclamation processes. Consequently, there has been a concerted effort since the 1960s to develop salt-resistant cultivars as a means to mitigate the effects of salt stress (Dewey, 1962; Epstein & Jefferies, 1964). These efforts have yielded promising results, with salt-tolerant alfalfa and bread wheat lines undergoing successful on-farm trials (e.g. AZ-Germ Salt II alfalfa, (Dobrenz, Robinson, Smith, & Poteet, 1989); S24 spring wheat, (M. Ashraf & O'leary, 1996)). However, limited genetic diversity within most crop gene pools restricts further progress. To overcome this limitation, researchers have explored the introgression of genes from wild relatives. Tal & Shannon (1983) investigated salt tolerance by crossing cultivated tomato (*Solanum lycopersicum* L.) with three wild *Solanum* species. While the resulting hybrids exhibited longer stems than their parents under salt stress conditions, the dominance of stem elongation observed only in *S. pennellii* indicated that the trait is not inherited in a straightforward manner. Further inheritance studies and diallel analyses conducted in tomato (Lyon, 1941), rice (Moeljopawiro & Ikehashi, 1981), pigeon pea (Subbarao, Johansen, Rao, & Jana, 1990), and sorghum (Azhar & McNeilly, 1988) have revealed that both additive and dominant factors play significant roles in the inheritance of salt tolerance, rendering breeding for salt tolerance a multifaceted task. This, together with diverse plant responses to salinity and stage-specific resistance, makes traditional breeding for salt tolerance a multifaceted task (Flowers, 2004). However, advanced selection methods, such as high-throughput plant phenotyping, molecular markers, and

QTL analyses, hold promise for enhancing breeding efforts aimed at improving salt tolerance (Muhammad Ashraf & Foolad, 2007; Gill *et al.*, 2022).

Genetic engineering offers alternatives to address the limitations associated with traditional breeding methods. The manipulation of genes responsible for regulating ion transporters, osmotic regulators, and antioxidant activities has demonstrated promise in enhancing salt tolerance through the transgenic approach (Muhammad Ashraf & Akram, 2009). For instance, Xue *et al.* (2004) successfully introduced a vacuolar Na⁺/H⁺ antiporter gene from *Arabidopsis thaliana* into wheat, resulting in improved grain yield and biomass production during on-farm trials. The TaP5CR gene in wheat stimulates proline synthesis, a key molecule for plant stress response. When this gene was transferred to *A. thaliana*, the resulting transgenic plants exhibited increased root growth and proline overproduction under salt stress conditions (Ma *et al.*, 2008). Badawi *et al.* (2004) demonstrated that introducing a gene encoding a superoxide dismutase (SOD) enzyme from rice into tobacco plants improved photosynthetic activity under salt stress conditions. This highlights the potential of manipulating antioxidant activity to enhance plant resilience to salinity.

Grafting is a horticultural technique that involves selecting and matching the root and shoot based on desired traits. The roots play a determinant role in plant water uptake by mediating between the shoots and the soil. Therefore, rootstock selection plays a key role in plant tolerance to water-deficient abiotic stresses, such as salt stress (Colla, Roupael, Leonardi, & Bie, 2010; Etehadnia, Waterer, De Jong, & Tanino, 2008). Grafting is a successful strategy for ameliorating salt stress in vegetables, primarily due to their glycophytic nature (Shannon & Grieve, 1998). A study, examining two *C. melo* varieties grafted onto three *Cucurbita maxima* Duch. × *Cucurbita moschata* Duch. rootstock cultivars, found a positive effect on the development of physiological mechanisms for mitigating salt stress, attributed to the regulation of Na⁺, Cl⁻, and K⁺ ions (L. Romero, Belakbir, Ragala, & Ruiz, 1997). Conversely, a separate study found no significant improvement in salt tolerance for grafted melons, although grafting returned higher profit potentially due to other benefits associated with fruit quality (Colla *et al.*, 2005).

1.7. Plant Growth Promoting Bacteria

A diverse community of soil microorganisms residing in close proximity to plant roots have been identified to facilitate plant development, optimize nutrient acquisition, and contribute to a thriving plant ecosystem (Adesemoye & Kloepper, 2009). Arbuscular mycorrhizal fungi (AMF), rhizobial N-fixing bacteria (RNF), and plant growth promoting bacteria (PGPB) are the primary groups with proven growth-promoting effects (Barea *et al.*, 1998; Kloepper, Ryu, & Zhang, 2004; Vessey, 2003).

PGPB, specifically colonizing the rhizosphere, consist of facultative, symbiotic, endophytic, and cyanophytic forms (Glick, 2012; Kloepper & Schroth, 1978). Despite the differences in categorization, PGPB promote plant growth through common strategies: facilitating water and nutrient uptake or hormonal regulation as biofertilizers, or suppressing pathogens as biocontrol agents (Glick, 1995).

The PGPB group, comprising various genera, implements these strategies by means of diverse mechanisms. For instance, indole-3-acetic acid (IAA), an auxin class hormone, demonstrably stimulates cell division and elongation, particularly within the root zone (Fu *et al.*, 2015). Notably, numerous PGPB strains synthesize and secrete IAA, enhancing root development (Patten & Glick, 1996). This, in turn, increases root exudates containing tryptophan, a vital IAA precursor, creating a positive feedback loop that benefits plant growth (B. Ali, Sabri, & Hasnain, 2010; Glick, 2014). Inoculation with IAA-producing *Bacillus* sp. resulted in a significant 37% increase in potato shoot elongation and enhanced plant root morphology (Ahmed & Hasnain, 2010). Endophytic bacteria, like *B. amyloliquefaciens*, can also produce auxins in addition to abscisic acid (ABA) (Çakmakçı, Mosber, Milton, Alatürk, & Ali, 2020). ABA, a stress-related phytohormone, induces stomatal closure to limit water loss during stressful conditions. However, this closure also restricts CO₂ uptake, thereby limiting plant growth (Abdelaal *et al.*, 2021). A study investigating an ABA-producing *B. amyloliquefaciens* strain found that rice plants inoculated with this bacterium showed reduced endogenous ABA under salinity stress (Shahzad *et al.*, 2017). This suggests the bacteria might benefit plants through an alternative pathway, potentially allowing for balanced water management and CO₂ uptake. Cytokinins and gibberellins produced by certain PGPB genera, including *Bacillus*, *Rhizobia*, and *Azotobacter*, are also noteworthy (Arkhipova, Veselov, Melentiev,

Martynenko, & Kudoyarova, 2005; Deka, Deka, & Baruah, 2015; Dodd, Zinovkina, Safronova, & Belimov, 2010). These hormones function as collaborators for plants under stress, stimulating the cellular differentiation, apical meristem activity, and even enhancing photosynthesis. Research suggests that bacterially derived forms have the potential to supplement a plant's endogenous hormone levels, thereby further enhancing its stress tolerance (G.-L. Wang, Que, Xu, Wang, & Xiong, 2015). Supporting this, Xu, Li, & Luo (2012) genetically modified *Sinorhizobium* strains to overexpress cytokinin genes. Inoculation with these strains enhanced alfalfa drought tolerance, via upregulating antioxidant enzymes such as dehydroascorbate reductase, catalase, and glutaredoxin.

In contrast, excess ethylene production during stress acts as a growth inhibitor (Apelbaum & Yang, 1981). Certain PGPB strains can counteract this ethylene-mediated stunting by producing ACC (amino cyclopropane carboxylate) deaminase. This enzyme catalyzes the breakdown of ACC, a precursor molecule for ethylene, thereby restricting the production of stress-related ethylene (Jacobson, Pasternak, & Glick, 1994; Zahir, Munir, Asghar, Shaharoona, & Arshad, 2008; Zarei, Moradi, Kazemeini, Akhgar, & Rahi, 2020). Moreover, ACC deaminase activity augments the efficacy of other growth-promoting factors, such as auxin, in the presence of stressors (Olanrewaju, Glick, & Babalola, 2017). A study investigated the impact of *Pseudomonas* endophytes with ACC deaminase enzyme on the growth of tomato plants under high salt conditions (S. Ali, Charles, & Glick, 2014). The inoculated plants exhibited enhanced growth, reduced stress-related ethylene production, limited salt accumulation, and increased chlorophyll content, indicating an enhanced photosynthetic efficiency under salt stress.

One additional strategy employed by plant growth-promoting bacteria (PGPB) is to enhance mineral uptake in plants. Nitrogen (N), the most critical mineral element after carbon, hydrogen, and oxygen, is essential for photosynthesis, hormonal homeostasis, and overall plant growth and development (Anas *et al.*, 2020). However, atmospheric nitrogen (N₂) primarily exists in a form unavailable for direct plant uptake. Certain PGPB strains, such as *Rhizobium* and *Azotobacter*, establish symbiotic relationships with plants by fixing atmospheric dinitrogen and converting it into ammonia (NH₃), readily absorbed by plants (Gage, 2004). Multiple research studies have consistently demonstrated the positive impact of N-fixing bacteria on plant N content, biomass, and crop yields in both

nodulating and non-nodulating plant species (Bai, Pan, Charles, & Smith, 2002; Gaspareto *et al.*, 2023; Kuan, Othman, Rahim, & Shamsuddin, 2016; Saubidet, Fatta, & Barneix, 2002). Similarly, phosphorus (P) is an essential macronutrient involved in the structure of the lipid bilayer, ATP and nucleic acids, and is also critical for various plant physiological processes, including enzyme activation and stomatal function (F. Khan, Siddique, Shabala, Zhou, & Zhao, 2023). A significantly large portion of soil phosphorus exists in insoluble forms unavailable for plant uptake. Notably, PGPB species belonging to the genera *Bacillus*, *Pseudomonas*, and *Serratia* can solubilize this bound phosphorus by lowering the soil pH (Rodríguez & Fraga, 1999). This process increases the bioavailability of phosphorus for plant root absorption. A significant increase in both available phosphorus and mycorrhizal root colonization of maize plants was observed following treatment with *P. fluorescens* (Krey, Vassilev, Baum, & Eichler-Löbermann, 2013). Iron (Fe) plays a vital role in plant metabolism, including the photosynthetic electron transport chain and cofactor activation (Kroh & Pilon, 2020). However, plants cannot utilize the most common form of iron in soil (ferric hydroxides, $\text{Fe}(\text{OH})_3$). In this context, siderophores, small, high-affinity iron-chelating molecules produced by PGPB, fungi, and even plants themselves, facilitate iron acquisition (Miethke & Marahiel, 2007). These siderophores chelate iron and form soluble iron-siderophore complexes readily taken up by plant roots. A case in point is the co-inoculation with siderophore-producing bacteria in a *C. melo* cultivar (Murgese, Santamaria, Leoni, & Crecchio, 2020). This upregulated the expression of iron transport and uptake genes, potentially leading to enhanced photosynthesis.

Beyond facilitating water and nutrient uptake or hormone regulation as biofertilizers, plant growth-promoting bacteria (PGPB) also function as biocontrol agents, suppressing a range of plant pathogens. The genera *Bacillus* and *Pseudomonas* are well-known producers of antibiotic metabolites (Olanrewaju *et al.*, 2017). A study demonstrated that *B. cereus* inhibited the growth of common plant pathogens in the *Fusarium* genus by producing hydrolytic enzymes such as chitinase, which degrades fungal cell walls (Chang, Chen, & Jao, 2007). Additionally, it promoted the overall growth of Chinese cabbage. Treatment with a specific strain of *Pseudomonas*, a beneficial soil bacterium known for its antibiotic properties targeting plant roots, has shown effectiveness against a wheat root rot disease

via producing the antibiotic phenazine-1-carboxylic acid (Bull, Weller, & Thomashow, 1991). 2,4-Diacetylphloroglucinol (DAPG) is another key antibiotic metabolite produced by certain strains of *P. fluorescens* (Handelsman & Stabb, 1996). Research has shown that DAPG suppresses root diseases, including black root rot of tobacco and take-all of wheat (Keel *et al.*, 1992). Similar suppressive effects of DAPG have been observed against damping-off of sugar beet and the potato cyst nematode (Cronin *et al.*, 1997; Dunne *et al.*, 1998). PGPB also have the potential to compete with pathogens for root colonization, thereby limiting pathogen growth. A study by Innerebner, Knief, & Vorholt (2011) demonstrated that beneficial strains of *Sphingomonas* and the pathogen *P. syringae* exhibited similar use of carbon sources for energy. This overlap in resource utilization by *Sphingomonas* and *P. syringae* likely creates competition, ultimately limiting resources available for the pathogen. Supporting this concept, a more motile and competitive variant of *Pseudomonas* showed improved control of fungal pathogens *Fusarium* and *Phytophthora* compared to its original form, although mutated for antibiotic synthesis (Barahona *et al.*, 2011). Furthermore, volatile compounds produced by PGPB can induce systemic resistance in plants. Volatiles from a strain of *Bacillus* increased resistance against black shank and target spot diseases in tobacco plants by inducing the expression of disease resistance genes (Kim *et al.*, 2015).

PGPB offer a sustainable and ecological alternative to synthetic fertilizers and pesticides due to their multifaceted mechanisms that not only promote plant growth but also mitigate the negative effects of abiotic stresses (Arora, Tewari, Singh, Lal, & Maheshwari, 2012). For instance, inoculation with *B. subtilis* significantly boosted potato growth rates by 13% and 8% under moderate and severe drought stress, respectively (Batool *et al.*, 2020). This enhanced growth was accompanied by a reduction in yield losses (17% and 15%) and improved cellular health under drought conditions, as evidenced by higher relative water content and membrane stability index in *B. subtilis* treated plants. These findings suggest that PGPB can enhance stress defense and reduce membrane damage in plants exposed to drought. Similarly, PGPB are being investigated for their ability to mitigate stress in plants exposed to extreme temperatures. Optimal growth typically occurs between 18-25°C, and deviations from this range (above 40°C or below 4°C) can induce stress. However, inoculation with *Burkholderia phytofirmans* can significantly alleviate chilling stress in

grapevines (Ait Barka, Nowak, & Clément, 2006). When exposed to cold temperatures (4°C), grapevine explants treated with PGPB exhibited over 10-fold enhanced root growth and more than doubled plant weight compared to non-inoculated controls. Furthermore, under chilling conditions, bacterized plants displayed a significant two-fold increase in both carbon assimilation and O₂ production compared to the control. Soybean plants exposed to heat stress at 40°C and inoculated with a thermotolerant *B. cereus* strain recovered from physiological and metabolic damage (M. A. Khan *et al.*, 2020). The inoculation with *B. cereus* resulted in an increase in chlorophyll, carotenoids, and salicylic acid (SA), while reducing the stress hormone (ABA). Additionally, *B. cereus* regulated the expression of heat shock proteins (HSP) over time and maintained potassium uptake and stress response genes under heat stress.

Inoculation with PGPB has been demonstrated to positively influence chlorophyll fluorescence in plants subjected to salt stress. Chlorophyll fluorescence parameters serve as indicators of the efficiency and health of the photosynthetic apparatus, particularly Photosystem II (PSII). For example, inoculation with the symbiotic fungus *Piriformospora indica* has been shown to enhance PSII efficiency and mitigate the negative effects of salt stress in tomato plants, as evidenced by improved F_v/F_m values (Ghorbani, Razavi, Ghasemi Omran, & Pirdashti, 2018). F_v/F_m is a parameter that reflects the maximum quantum efficiency of PSII, indicating reduced photoinhibition and oxidative stress. Similarly, inoculation with salt-tolerant PGPB strains from *Bougainvillea glabra* has been found to improve chlorophyll fluorescence parameters, such as F_v/F_m , in wheat and maize under salt stress, indicating enhanced photosynthetic performance and increased stress tolerance (Karnwal, 2020). This suggests enhanced photosynthetic performance and increased stress tolerance due to bacterial inoculation. Furthermore, AMF inoculation has been shown to enhance the photochemical efficiency of PSII and alleviate the adverse effects of water stress in cassava (Oyetunji, Ekanayake, & Osonubi, 2007), comparable to the beneficial effects of PGPB under salt stress.

While single-strain inoculations with PGPB have proven successful, recent research suggests that co-inoculation with multiple PGPB strains may offer even greater advantages. For example, a study investigating maize plants demonstrated that *P. putida* alone significantly enhanced drought tolerance by improving the fresh to dry mass ratio

by 6% and the percentage of dry matter by 7% (Kálmán, Nagy, Berényi, Kiss, & Posta, 2024). However, co-inoculation with both *B. pumilus* and *P. putida* resulted in a considerably more substantial increase in grain production (15%) under drought conditions. This observed synergy between the strains highlights the potential benefits of co-inoculation strategies. Similar findings were reported in chickpea plants, where both individual and co-inoculations with *P. putida* and *B. amyloliquefaciens* increased plant biomass under drought stress (Kumar *et al.*, 2016). Although both individual and co-inoculations increased plant biomass under water deficiency compared to non-inoculated plants, the co-inoculation was particularly effective in mitigating drought stress. This was evidenced by the similar SOD activities of the co-inoculated plants with the controls, indicating a complete alleviation of drought stress by the combined action of both bacterial strains. The potential of co-inoculation strategies extends beyond drought stress mitigation. A study employing a *Bacillus-Serratia* consortium significantly enhanced tomato plant tolerance against chilling stress (C. Wang, Wang, Gao, Wang, & Guo, 2016). The plants treated with the consortium exhibited a 77% higher survival after chilling and recovery compared to the non-inoculated controls. Inoculation with the consortium appears to activate plant defense mechanisms, by an initial stimulation of MDA and H₂O₂ production followed by a reduction in these markers, suggesting a subsequent decrease in membrane damage. Heavy metal contamination in soil represents another significant abiotic stress factor that threatens plant growth and development. A greenhouse study investigated whether a co-inoculum of heavy metal-tolerant *Alcaligenes faecalis* and *B. cereus* could mitigate heavy metal (Cu, Cd, Pb, Zn) toxicity in sorghum (El-Meihy, Abou-Aly, Youssef, Tewfike, & El-Alkshar, 2019). Inoculation significantly enhanced sorghum tolerance by increasing peroxidase and polyphenol oxidase activity, chlorophyll and carotenoid production, and reducing metal absorption. Notably, these bacteria also promoted translocation of metals from roots to shoots. This effect is likely due to their production of chelating agents, such as siderophores, which can bind and mobilize heavy metals within the plant.

Previous studies have shown that *Bacillus* species can reduce salt stress in tomato (Cordero, Balaguer, Rincón, & Pueyo, 2018), wheat (Nawaz *et al.*, 2020; Upadhyay, Singh, Saxena, & Singh, 2012), radish (Mohamed & Gomaa, 2012; Yildirim, Donmez, &

Turan, 2008), and soybean (Estévez, Dardanelli, Megías, & Rodríguez-Navarro, 2009). While *Bacillus* has been studied for its effects in melon for fungal diseases (Antonelli, Reda, Aleandri, Varvaro, & Chilosi, 2013; García-Gutiérrez *et al.*, 2012; D. Romero *et al.*, 2007; Singh, 2021) and plant growth (Kang *et al.*, 2015; Zhao *et al.*, 2011), no research has been conducted on its impact on salt stress. A study investigating the co-inoculation of PGPB strains from the genera *Enterobacter* and *Pseudomonas* evaluated their effects on *C. melo* plants under reduced fertilizer application. The inoculation significantly increased yield by increasing total fruit number and sugar content. Additionally, it enhanced transpiration capacity in terms of chlorophyll content and stomatal conductance. The study found that PGPB can potentially reduce the reliance on synthetic fertilizers, as evidenced by higher sugar and chlorophyll levels at lower fertilizer inputs (Murgese *et al.*, 2020).

1.8. Seed Priming

Priming is a pre-sowing hydration treatment that involves the use of pure water, various salts, and chemicals. Its main objectives are to enhance the germination rate and speed, increase plant tolerance to various environmental conditions, and ensure homogeneity in seedlings. Priming is a process that involves soaking seeds in moisture to initiate their pre-germination metabolic activity, without allowing for radicle emergence, and then drying them back to storage moisture (Copeland & McDonald, 2001). This process prepares the seeds for germination by performing the necessary metabolic activities, cell and DNA repair activities, mRNA and protein synthesis before sowing (Bewley, Bradford, Hilhorst, & Nonogaki, 2013). Numerous studies have demonstrated that priming with NaCl solution enhances plants' tolerance to salt stress. The plant species investigated in these studies include tomato (Cayuela, Pérez-Alfocea, Caro, & Bolarín, 1996), melon (N. Sivritepe *et al.*, 2003a), cucumber (Esmailpour, Ghassemi-Golezani, Khoei, Gregoorian, & Toorchi, 2006), onion (H. O. Sivritepe & Sivritepe, 2007), safflower (Elouaer & Hannachi, 2012), pea (Şentürk & Sivritepe, 2016), and sorghum (Xiaofei Chen *et al.*, 2021a).

In this thesis, a salt-sensitive melon cultivar, *Cucumis melo* cv. Hasanbey (H. O. Sivritepe, Eris, & Sivritepe, 1999) will be treated with NaCl-seed priming and halotolerant PGPB (Plant Growth-Promoting Bacteria) inoculum during seedling stage. While improving seed adaptation and performance with NaCl-priming under saline conditions (Cayuela *et*

al., 1996; Xiaofei Chen *et al.*, 2021a; Elouaer & Hannachi, 2012; N. Sivritepe, Sivritepe, & Eris, 2003), the following growth stages will be supported with halotolerant PGPB inoculants (Cordero *et al.*, 2018; Sharma, Kulkarni, & Jha, 2016; Upadhyay *et al.*, 2012). Plant Growth Promoting Bacteria, or in a broad sense, bio-formulations, are environmentally friendly methods to support plant growth and mitigate abiotic stresses. Plant Growth Promoting Bacteria, offer a sustainable alternative to synthetic agrochemicals under adverse growth conditions (Arora *et al.*, 2012). A variety of rhizobacteria genera (*Achromobacter*, *Arthrobacter*, *Azospirillum*, *Bacillus*, *Paenibacillus*, *Phyllobacterium*, *Pseudomonas*) may be used to alleviate abiotic stresses in different plant species (Goswami & Deka, 2020; Jalal *et al.*, 2023). Our study specifically focused on *Bacillus* species, which have been proven to alleviate salt stress in tomato (Cordero *et al.*, 2018), wheat (Nawaz *et al.*, 2020; Upadhyay *et al.*, 2012), radish (Mohamed & Gomaa, 2012; Yildirim *et al.*, 2008), and soybean (Estévez *et al.*, 2009). Nevertheless, there is a noticeable gap in the literature regarding Plant Growth Promoting Bacteria (PGPB), treatments for melon cultivation under saline conditions. The aim of this thesis is to address this knowledge gap by introducing a novel perspective on salinity studies. This will be achieved by integrating plant growth-promoting bacteria (PGPB) inoculation with NaCl-seed priming on a salt-sensitive melon variety. The effects on seedling development and plant physiology will be investigated.

Seed priming and PGPB (Plant Growth-Promoting Bacteria) applications are both sustainable methods used to enhance plant tolerance to abiotic stresses such as salt stress. However, these methods are applied at different growth phases of the plant. Quantitative Trait Locus (QTL) mapping studies in *Triticeae* and tomato species have shown that QTL sets associated with tolerance at different phenophases mostly do not intersect (Cattivelli *et al.*, 2002; Foolad, 1999). This suggests that distinct genetic mechanisms govern the salt tolerance mechanisms of germination and vegetative growth stages. Although tolerance during germination, the critical initial phase of the plant's lifecycle, holds greater importance, addressing salt stress through alleviating treatments in subsequent phenological stages remains significant. Recognizing this distinction underscores the importance of implementing multi-stage strategies to combat salt stress in plants throughout their growth cycle.

The only study we identified that combined seed priming and PGPB applications was conducted by Mehboob *et al.* (2022). They investigated the effects of boron deficiency on chickpea (*Cicer arietinum* L.) using seed priming with boron and bacterial inoculation with *Bacillus* sp. However, their study focused on germination and yield parameters. This thesis is unique in that it uses the halopriming with NaCl, aims to improve salt stress tolerance, and focuses more on physiological and photosynthetic parameters as well as morphological parameters.



2. MATERIALS & METHODS

2.1. Plant Material and PGPB Strains



Figure 2.1. Jar of Hasanbey-1 melon seeds in a lab setting.

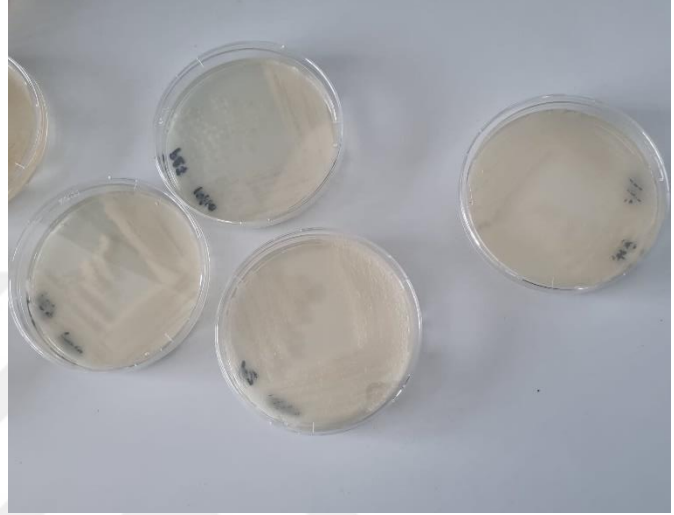


Figure 2.2. Petri dishes containing *Bacillus* sp. microbial cultures.

Certified melon seeds (*Cucumis melo* L.) of Hasanbey cultivar, previously identified as salt-sensitive in a study by Sivritepe, Eris, and Sivritepe (1999), were obtained from BETA Agriculture Trade Inc (Figure 2.1).

The PGPB strains used in this experiment were obtained from the Molecular Microbiology (MMB) Research Group at Konya Food & Agriculture University (Figure 2.2). Eight different *Bacillus* sp. strains were provided, designated X4, X5, PR8, P2, PR10, PR7, PR9, and M8.

The sand used in the pot experiment was sourced from the top 0-20 cm layer within the campus grounds of Konya Food & Agriculture University. The sand was sieved before use. The compost component of the soil mixture was obtained commercially from Klasmann-Deilmann GmbH, Geeste, Germany.

2.2. Seed Tests and Seed Priming

2.2.1. Thousand-Seed Weight Determination

Thousand-seed weight (TSW) of the melon seeds was determined according to the International Seed Testing Association (ISTA) Rules (ISTA, 2023c) by counting 8

replicates of 100 seeds. The seeds were counted, and each replicate individually weighed on the precision balance (Precisa BJ 100M) having an accuracy at ± 0.001 g. The TSW was calculated using the below formula:

$$TSW = \frac{\sum \text{Weight of 100 seeds}}{\text{Number of replicates}} \times 10 \quad (2.1)$$

2.2.2. Seed Moisture Content Determination

Seed moisture content was determined following the ISTA Rules (ISTA, 2023b) using the high-constant-temperature method. Two replicates of glass Petri dishes (8 cm diameter) with lids were weighed to the nearest 0.001 g (M_1). Subsequently, 5.0 ± 0.01 g of melon seeds were added to each Petri dish, and the weight was recorded again (M_2). The Petri dishes, either placed on top of their lids or beside them, were immediately transferred to an oven set at $130\text{--}133$ °C for precisely 1 hour $\pm$ 3 minutes. After drying, the Petri dishes were covered with their lids and transferred to a desiccator to cool down to room temperature. Once cooled, the dishes along with their lids and contents were weighed again (M_3). The moisture content ($W\%$) was calculated using the following equation:

$$W\% = \frac{M_2 - M_3}{M_2 - M_1} \times 100 \quad (2.2)$$

where

M_1 : Pre-drying weight of a Petri dish and lid (g)

M_2 : Pre-drying weight of a Petri dish, lid, and seeds (g)

M_3 : Post-drying weight of a Petri dish, lid, and seeds (g)

$M_2 - M_1$: Seed weight (g)

$M_2 - M_3$: Weight loss (g)

2.2.3. Seed Priming



Figure 2.3. Melon seeds undergoing priming in a 0.9% (150 mM) NaCl solution, with a seed to solution ratio of 1:5 (w/v).

Melon seeds were primed using a 0.9% (150 mM) NaCl solution. The seed to solution ratio was maintained at 1:5 (w/v). Seeds were soaked in the solution for 16 hours at $16 \pm 1^\circ\text{C}$ in a cooled incubator under dark conditions (Dhillon, 1995; H. O. Sivritepe *et al.*, 1999). Following incubation, the seeds were thoroughly rinsed with distilled water to remove residual NaCl solution. The rinsed seeds were then air-dried at room temperature and stored at 4°C for subsequent use. Untreated seeds were used as the control group for the germination and pot experiments.

2.2.4. Seed Germination Test



Figure 2.4. One repetition of the germination test prepared according to ISTA rules to evaluate the effects of NaCl-priming and salt stress on seed germination.

The effects of NaCl-priming and salt stress on seed germination were evaluated using a germination test following the ISTA Rules (ISTA, 2023a). The between-paper method was employed. Seeds were placed between moistened paper towels, which were then wrapped in plastic bags and positioned upright in a cooled incubator. Each replicate contained 25 seeds,

with eight replicates per treatment group. Seeds germinated under a photoperiodic lighting regime (16 hours light/8 hours dark) at 25°C with a relative humidity of around 40%.

Four treatment groups were established to assess the impact of salt stress and NaCl-priming on melon seed germination (Table 2.1). Germination media for the non-stressed control groups (NP and P) were moistened with distilled water. Conversely, media for the salt-stressed groups (NPS and PS) were moistened with a 0.9% NaCl solution.

Table 2.1. Description of treatment groups for seed germination test.

<i>Treatment</i>	<i>Description</i>	<i>Germination Media</i>
<i>NP</i>	Non-primed, non-stressed	Distilled water
<i>NPS</i>	Non-primed, salt-stressed	0.9% NaCl solution
<i>P</i>	Primed, non-stressed	Distilled water
<i>PS</i>	Primed, salt-stressed	0.9% NaCl solution

Germinated seeds were counted and recorded daily for 10 days. Seedlings with the potential to develop into a normal plant under favorable conditions were considered normal germination. These seedlings exhibited intact primary root, hypocotyl, and cotyledon tissues, with slight defects allowed. Seedlings lacking this potential were classified as abnormal germination. Ungerminated seeds were recorded as dead. The total germination rate was determined by the percentage of normally germinated seeds from each replicate across the experiment. Seedling fresh weight was measured for each replicate at the conclusion of the germination test. Germination Index, GI (2.3) (Maguire, 1962) and Mean Germination Time, MGT (2.4) (Ellis, 1981) were calculated as below:

$$GI = \sum \frac{n}{d} \quad (2.3)$$

$$MGT = \frac{\sum d*n}{\sum n} \quad (2.4)$$

where:

n: The number of normal seedlings on day d

d: Days counted from the beginning of germination test

2.3. Bacterial Culture Preparation and Salt Tolerance Assay

2.3.1. Bacterial Culture Expansion

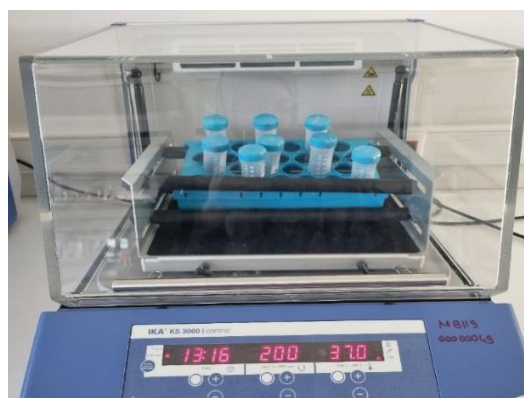


Figure 2.5. Incubation of single colonies in 20 mL LB broth at 200 rpm and 37°C.

Eight *Bacillus* sp. strains were retrieved from cold storage and streaked onto solid Luria-Bertani (LB) agar plates for isolation. The plates were incubated for 24 hours at 37°C to promote bacterial growth. A single colony from each strain was transferred to a 2 mL LB broth medium and incubated overnight in a shaking incubator at 200 rpm and 37°C.

Subsequently, 200 μ L aliquots of these overnight cultures were inoculated into separate 20 mL LB broth cultures and incubated again under the same conditions for 7 hours (Figure 2.5). The cultures were then centrifuged at 10,000 rpm for 5 minutes to pellet the bacterial cells. The supernatant was discarded, and the cell pellets were resuspended in 5 mL of sterile 0.9% NaCl solution.

2.3.2. Minimum Inhibitory Concentration (MIC) Assay

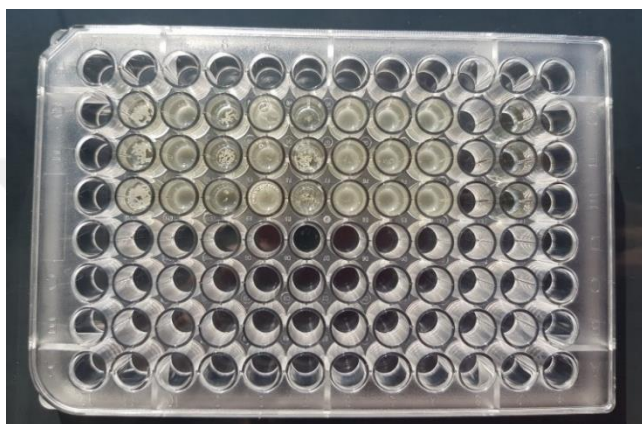


Figure 2.6. 96-well microplate for MIC assay with 200 μ L LB broth at 1%, 6%, 8%, or 10% salt concentrations.

Salt tolerance of *Bacillus* sp. strains was assessed using a minimum inhibitory concentration (MIC) assay. Building on previous salt tolerance studies with *Bacillus* sp. (Cordero *et al.*, 2018; Upadhyay *et al.*, 2012), three salt concentrations (6%, 8%, and 10%) were chosen to differentiate the tolerance levels among the bacterial strains. As LB

broth inherently contains 1% NaCl, the control group was set at this concentration. To achieve the desired final salt concentrations in the test broths, the inherent 1% NaCl content was factored in during media preparation.

96-well microplates were used for the MIC assay. Each well received 200 μ L of LB broth medium prepared at one of the four salt concentrations (1%, 6%, 8%, or 10%). Three replicate wells were prepared for each bacterial strain and each salt concentration. Twenty microliters of the resuspended bacterial cultures were inoculated into each well (approximately 10^5 CFU/well). Negative controls consisted of three replicate wells containing only LB broth medium at the control concentration (1%) without bacterial inoculation. The microplates were incubated at 37°C overnight.

2.3.3. Bacterial Growth Evaluation and Selection of Salt-Tolerant Strains

Bacterial growth was evaluated by measuring the optical density (OD) at 600 nm from the microplates the following day. The five *Bacillus* sp. strains exhibiting the highest OD values in the presence of increasing salt concentrations were selected for further studies. While a direct conversion of OD to CFU/mL is not recommended due to factors like

growth phase and culture conditions, a commonly accepted conversion factor of $0.5 \text{ OD}_{600} \approx 10^8 \text{ CFU/mL}$ for *Bacillus* sp. can be used for a preliminary estimation (Ghosh & Setlow, 2009). Additionally, to verify OD readings, a 5 mL aliquot from one of the bacterial cultures was diluted in 45 mL of NaCl solution (0.9%) and plated onto LB agar medium (100 μL per plate). The plate was incubated at 37°C overnight, and colony-forming units (CFUs) were counted the next day. The bacterial concentration (CFU/mL) was determined using the following equation:

$$\text{CFU/mL} = \frac{(\text{No. of colonies} \times \text{Dilution factor})}{\text{Volume of culture plated}} \quad (2.5)$$

2.3.4. Inoculum Preparation for Plant Application

The five selected bacterial strains (PR9, M8, X4, X5, PR8) were retrieved from cold storage and streaked onto separate LB agar plates. The plates were incubated for 24 hours at 37°C . Following incubation, a single colony from each strain was inoculated into a 2 mL LB broth medium and incubated overnight in a shaking incubator at 200 rpm and 37°C . Approximately 18 hours after inoculation, 200 μL aliquots of the overnight cultures were transferred to separate 20 mL LB broth cultures and incubated in a shaking incubator at 200 rpm and 37°C for 6 hours. The cultures were then centrifuged at 10,000 rpm for 5 minutes to pellet the bacterial cells. The supernatants were discarded, and the cell pellets were resuspended with a 1 mL of sterile NaCl solution (0.9%).

For optical density (OD) measurements at 600 nm, the resuspended bacterial cultures were diluted 1:100 with sterile NaCl solution. The $0.5 \text{ OD}_{600} \approx 10^8 \text{ CFU/mL}$ conversion factor was used to estimate the bacterial concentration in the original cultures.

To minimize potential negative synergistic effects, the five resuspended strains were mixed immediately before transplantation. The combined volume of the bacterial suspension was approximately 5 mL ($5 \times 10^9 \text{ CFU/mL}$). The mixture was further diluted with sterile water to achieve a final volume of 70 mL (considering 2 mL of solution would be added to each of the 32 pots). During transplantation, 2 mL of the final diluted bacterial solution was added to the root zone of each plant.

2.4. Pot Experiment and Growth Conditions

The pot experiment was conducted in the greenhouse at Konya Food and Agriculture University from October to December 2023. Temperature and relative humidity data were logged every 30 minutes using a datalogger (Cem DT-172). The average temperature throughout the experiment was 20 °C, and the average relative humidity was recorded as 49%.

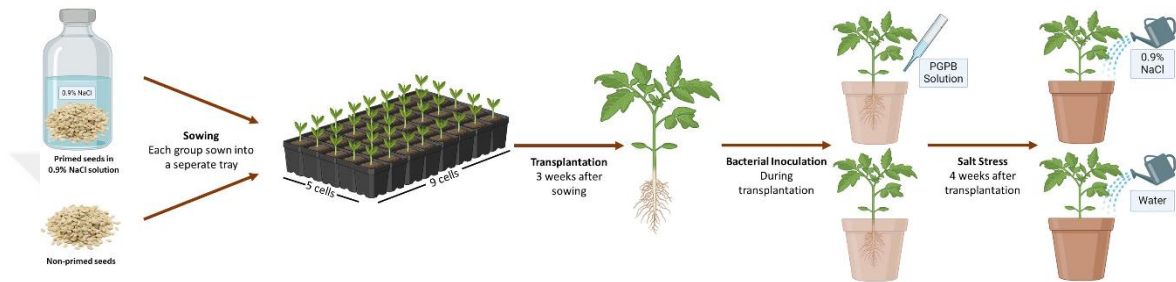


Figure 2.7. A schematic illustration of the experimental timeline for investigating the effects of seed priming with NaCl solution and PGPB inoculation under salt stress on melon plants grown in pots (Created with Biorender.com).

2.4.1. Seed Germination



Figure 2.8. Seedling trays (9 x 5) filled with compost, with primed and non-primed seeds sown in separate cells.

Primed and non-primed seeds were sown in separate 9 x 5 seedling trays filled with compost (Figure 2.7). To ensure sufficient seedlings for the experiment, two seeds were sown per cell. Trays were irrigated daily with equal amounts of distilled water throughout the germination period.

2.4.2. Field Capacity Determination

The field capacity (FC) of the potting mix was determined using two pots representative of those used in the experiment. Pots were weighed after filling with the soil mixture (10% compost and 90% sand). The pots were then saturated with water and weighed again after 48 hours. FC was calculated using the following equation:

$$FC = M_2 - M_1 \quad (2.6)$$

where:

M₁: Dry weight of the pot containing the soil mixture (g)

M₂: Weight of the pot containing the soil mixture after 48 hours of saturation (g)

2.4.3. Transplantation and Pot Preparation

After three weeks, seedlings were transplanted into individual 3 L-pots. The inner surface of each pot was lined with filter paper to prevent soil loss. The potting mix consisted of 10% compost and 90% sand. During transplanting, PGPB solution (approximately 10⁹ CFU/mL) was applied to the root zone of inoculated treatments (Figure 2.7).

On the first day of transplanting, non-bacteriated groups received 200 mL of water, while pots containing the bacterial solution received 100 mL to prevent dilution. Subsequently, all groups were irrigated daily with 80 mL of distilled water for four weeks to allow for seedling establishment before salt stress application.

Seedlings were fertilized with 10.30.10+ME NPK solution twice during this period (days 10 and 20 post-transplantation), applied with irrigation water.

2.4.4. Salt Stress Application and Evapotranspiration Measurement

After a four-week growth period with regular watering, salt stress was imposed on designated groups. These groups were irrigated with a 0.9% NaCl solution every other day for 3 weeks. Control groups continued to receive distilled water throughout this period (Figure 2.7). The amount of water transpired by the plants (evapotranspiration, ET) was estimated by weighing the pots before each irrigation event (Figure 2.9). Weight data were recorded for each watering. Since the pots had equal surface areas, the difference in weight between irrigations reflects the amount of water transpired by the plants and evaporated from the soil surface. This difference was used as an indicator of the effects of priming, bacteria inoculation, and salt stress on plant water use. The volume of water applied during



Figure 2.9. A pot weighed before irrigation to estimate water loss.

irrigation corresponded to 55% of the pre-determined field capacity, ensuring plants were not waterlogged while still allowing for measurable water loss. A single preventative copper solution spray was applied to all plants midway through the salt stress period to control powdery mildew. Additionally, all plants received a third dose of 10.30.10+ME NPK fertilizer mixed with irrigation water during this time.

The pot experiment evaluated the individual and combined effects of seed priming and PGPB inoculation on melon seedlings under salt stress (Figure 2.10). Eight treatments (eight replicates each) were arranged in a 2x2x2 factorial design:

- i. Seed Priming (P vs. Non-Primed)
- ii. Bacterial Inoculation (B vs. Non-Inoculated)
- iii. Salt Stress (S vs. No Stress)

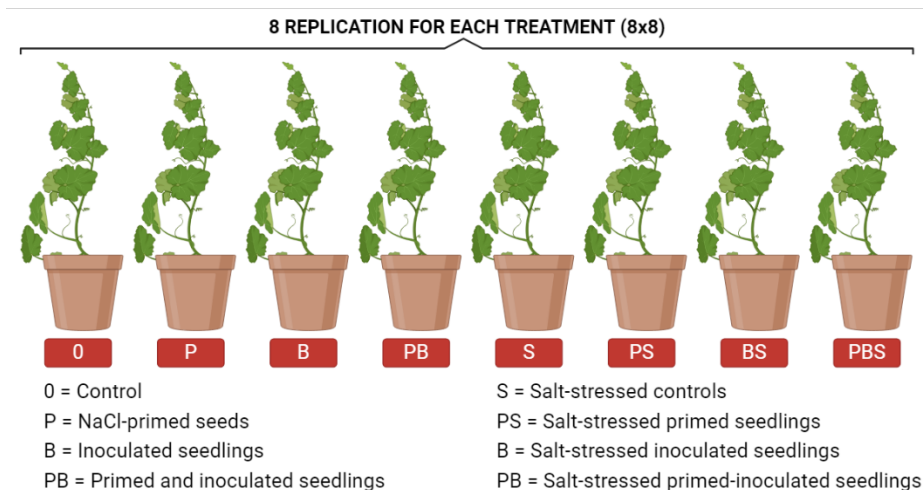


Figure 2.10. A schematic illustration of the experimental design for the pot experiment. The figure depicts all treatment groups and their assigned labeling system for clarity (Created with Biorender.com).

2.5. Plant Growth and Physiological Parameters

2.5.1. Plant Morphological Measurements

Plant height and the number of fully developed leaves were recorded every other day for one week prior to the initiation of salt stress and continued until harvest.

Plant shoot and root fresh weights were measured at harvest. Subsequently, the roots were dried at 80°C for 48 hours in an oven. The dried root weight was then measured and recorded.

A photograph of the fully developed third leaf from the top of each replicate was captured. Leaf area was then calculated using the ImageJ (Rasband, 1997; Schneider, Rasband, & Eliceiri, 2012).

2.5.2. Relative Membrane Permeability (RMP) Assay



Figure 2.11. Five small discs (approximately equal size) punched from each third leaf to assess RMP.

Five small discs (approximately equal size) were punched from each third leaf to assess relative membrane permeability (Yang, Rhodes, & Joly, 1996). Each leaf disc was placed individually in 20 mL of distilled water. Eight replicates were performed for each treatment group. Electrical conductivity (EC) was measured using a conductivity meter after vortexing the tubes for 5 seconds to disrupt the cell membranes (EC_0). The tubes were then incubated at 4°C for 24 hours. Following incubation, the samples were vortexed again to ensure even distribution, and a second EC measurement (EC_1) was taken. Finally, the tubes were autoclaved at 120°C for 20 minutes to achieve complete membrane permeability (EC_2). The relative membrane permeability (RMP%) was calculated using the following formula:

$$RMP (\%) = \frac{EC_1 - EC_0}{EC_2 - EC_0} \times 100 \quad (2.7)$$

where:

EC₀: The first electrical conductivity value of the sample (initial leakage)

EC₁: Electrical conductivity value of the sample after incubating for 24 h at 4°C

EC₂: Electrical conductivity value of the sample after autoclaving (maximum leakage)

2.5.3. Relative Water Content (RWC) Assay



Figure 2.12. Leaves placed in plastic bags filled with water, ensuring complete submersion of the leaf petioles.

Second youngest fully developed leaves from each plant were used for the relative moisture content (RWC) calculation (Slavik, 1974). Fresh weight (FW) of each leaf was measured. The leaves were then placed in plastic bags filled with water, ensuring complete submersion of the leaf petioles (Figure 2.12). Eight replicates were performed for each treatment group. The bags were incubated at 4°C for 24 hours. Following incubation, the leaves were carefully removed, and excess surface water was gently blotted with a paper towel to remove free-flowing water. Turgid weight (TW) was then

measured for each leaf. Finally, the leaves were dried at 80°C for 24 hours in an oven, and dry weight (DW) was measured. The relative water content (RWC) was calculated using the following formula:

$$RWC (\%) = \frac{FW - DW}{TW - DW} \times 100 \quad (2.8)$$

where:

FW: Fresh weight of the leaf sample (g)

TW: Turgid weight of the leaf sample after incubation at 100% humidity (g)

DW: Dry weight of the leaf sample after oven drying (g)

2.6. Plant Photosynthetic Measurements

Photosynthetic parameters were measured throughout the experiment, starting at the initiation of salt stress and continuing until harvest. Measurements were taken every other day between 10:00 and 12:00 PM from the second most developed leaf from the top on each replicate.



Figure 2.13. Experimental setup in the greenhouse, showing melon plants in pots.

2.6.1. Dark-Adapted Chlorophyll Fluorescence

A Pocket Plant Efficiency Analyzer (PEA, Hansatech Instruments Ltd., King's Lynn, UK) was used to measure chlorophyll fluorescence parameters following a 20-minute dark adaptation period. These parameters provide insights into the efficiency of photosystem II (PSII) function (Kalaji *et al.*, 2016; R. J. Strasser, Tsimilli-Michael, & Srivastava, 2004).

- **Minimum fluorescence (F_0) and maximum fluorescence (F_m):** These parameters represent the minimum and maximum fluorescence yield of photosystem II (PSII) reaction centers (RC) in a dark-adapted state.
- **Effective absorption flux per reaction center (ABS/RC):** This parameter reflects the light absorbed by functional reaction centers. It was calculated using the formula:

$$ABS/RC = \frac{1 - Chl_{RC}/Chl_{tot}}{Chl_{RC}/Chl_{tot}} \quad (2.9)$$

where:

Chl_{RC} : Chlorophyll associated with reaction centers

Chl_{tot} : Total chlorophyll content

- **Electron transport rate (ETR) beyond plastoquinone-A (ET_o/RC):** This parameter reflects the electron transport activity beyond plastoquinone-A per reaction center. It was calculated using the formula:

$$ET_o/RC = \frac{1}{V_J} \times M_o \times \psi_o \quad (2.10)$$

where:

M_o: Constant

V_J: Relative volume of the electron transport chain judged to be operating

Ψ_o: Specific electrical conductivity across the thylakoid membrane in the light-adapted state

- **Performance index on an absorption basis (PI_{ABS}):** This parameter provides a comprehensive assessment of PSII functionality, incorporating photochemical and non-photochemical processes. It was calculated using the formula:

$$PI_{ABS} = RC/ABS \times \frac{\phi P_o}{1 - \phi P_o} \times \frac{\psi E_o}{1 - \psi E_o} \quad (2.11)$$

where:

RC/ABS: Probability of an excitation energy being trapped by a reaction center

ϕP_o: Maximum quantum yield of PSII primary photochemistry

ΨE_o: Efficiency with which an electron is transported beyond the plastoquinone-A pool per absorbed photon

- **Maximum quantum yield of PSII primary photochemistry (ΦP_o, F_v/F_m):** This parameter reflects the probability that an absorbed photon will be trapped by the PSII reaction center. It was measured in dark-adapted samples using the formula:

$$\psi P_o = F_v/F_m = 1 - \frac{F_o}{F_m} \quad (2.12)$$

where:

F_v: Variable fluorescence

F_m: Maximum fluorescence

- **OJIP Curve Analysis:** A polyphasic chlorophyll *a* (Chl *a*) fluorescence transient plotted on a logarithmic timescale. It reflects the dynamic behavior of photosystem II (PSII) following a brief, saturating light pulse. The fluorescence rise can be characterized by distinct steps denoted as O-J-I-P:

- **O (origin)** - Fluorescence intensity F_o (at 30 μs)

- **J** - Fluorescence intensities F_J (at 2 ms)
- **I** - Fluorescence intensities F_I (at 30 ms)
- **P (peak)** - Maximal fluorescence intensity, $F_P = F_M$

2.6.2. Gas Exchange and Light-Adapted Chlorophyll Fluorescence Parameters

A Li-600 porometer and fluorimeter (Li-Cor Inc., Lincoln, NE, USA) was used to measure gas exchange and light-adapted chlorophyll fluorescence parameters:

- **Stomatal conductance to water vapor (G_{sw} , mmol/m²s):** This parameter was determined by measuring the rate of water vapor released by a leaf inside a chamber. This transpiration rate is calculated based on the difference in water vapor concentration between the air entering and exiting the chamber.
- **Maximum fluorescence (F_m'):** The maximum fluorescence yield achievable in the light-adapted state.
- **Quantum efficiency in light (Φ_{PSII}):** This parameter reflects the proportion of light energy captured by PSII that drives electron transport. It was calculated using the following equation (Genty, Briantais, & Baker, 1989):

$$\phi_{PSII} = \frac{F_m' - F_s}{F_m'} \quad (2.13)$$

where:

F_m' : Maximum fluorescence yield in a light-adapted leaf

F_s : Steady-state fluorescence yield in a light-adapted leaf

- **Electron transport rate (ETR , $\mu\text{mol}/\text{m}^2\text{s}$):** This parameter reflects the linear rate of electron flow through the photosynthetic electron transport chain. Derived from chlorophyll fluorescence measurements, it is reported as the rate of electron transport per unit leaf area per unit time (Rascher, Liebig, & Lüttge, 2000).

$$ETR = \frac{F_m' - F_s}{F_m'} \times PPFD \times 0.5 \quad (2.14)$$

where:

PPFD: photosynthetically active photon flux density

F_m' : Maximum fluorescence yield in a light-adapted leaf

F_s : Steady-state fluorescence yield in a light-adapted leaf

- Leaf H₂O mole fraction ($H_{2O_{leaf}}$, mmol/mol)
- Leaf temperature (T_{leaf} , °C)

2.7. Statistical Analysis

The effects of seed priming, bacterial treatment, and salt stress (and their interactions) on seed germination, plant growth, and physiological parameters were analyzed using two-way analysis of variance (ANOVA) tests. Post-hoc comparisons to assess significant differences between treatment groups were performed using Duncan's multiple range test and the least significant difference (LSD) test. All analyses were conducted using either SPSS 27.0 (IBM Corp., Armonk, NY, USA) or GraphPad Prism 10.2 (GraphPad Software, San Diego, California USA). Prior to analysis, all data were checked for outliers in GraphPad Prism using the ROUT Method ($Q=1\%$) and any detected outliers were removed.

3. RESULTS & DISCUSSION

3.1. Seed Tests and Seed Priming

3.1.1. Thousand-Seed Weight Determination

$$TSW = \frac{\Sigma \text{Weight of 100 seeds}}{\text{Number of replicates}} \times 10 \quad (3.1)$$

$$TSW = \frac{3.56+3.67+3.55+3.47+3.55+3.56+3.54+3.59}{8} \times 10 \quad (3.2)$$

$$TSW = \frac{28.49}{8} \times 10 \quad (3.3)$$

$$TSW = 35.61 \quad (3.4)$$

3.1.2. Seed Moisture Content Determination

$$W\% = \frac{M_2 - M_3}{M_2 - M_1} \times 100 \quad (3.5)$$

where

M₁: Pre-drying weight of a Petri dish and lid (g)

M₂: Pre-drying weight of a Petri dish, lid, and seeds (g)

M₃: Post-drying weight of a Petri dish, lid, and seeds (g)

M₂ - M₁: Seed weight (g)

M₂ - M₃: Weight loss

Replicate 1:

$$W_1\% = \frac{62.978 - 62.554}{62.978 - 57.978} \times 100 \quad (3.6)$$

$$W_1\% = \frac{0.424}{5.000} \times 100 \quad (3.7)$$

$$W_1\% = 8.5 \quad (3.8)$$

Replicate 2:

$$W_2\% = \frac{63.354 - 62.927}{63.354 - 58.337} \times 100 \quad (3.9)$$

$$W_2\% = \frac{0.427}{5.017} \times 100 \quad (3.10)$$

$$W_2\% = 8.5 \quad (3.11)$$

$$W_{lot}\% = \frac{(W_1 + W_2)}{2} = 8.5\% \quad (3.12)$$

3.1.3. Seed Germination Test

The Non-Primed (NP) seeds exhibited a rapid increase in germination rate, reaching close to 100% by day 10. This suggests that under normal conditions, untreated seeds possess a

high potential for successful germination (Figure 3.1). The NaCl-Primed (P) seeds also demonstrated a sharp upward trend in germination rate, achieving results comparable to the NP seeds.

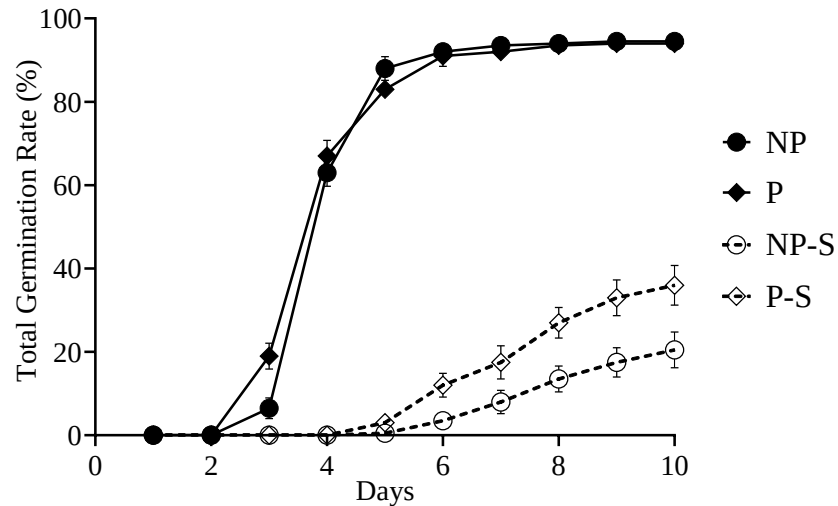


Figure 3.1. Time course of total germination rate of melon seeds over a period of 10 days. Non-Primed Seeds (NP, ●), NaCl-Primed Seeds (P, ◆), Non-Primed+Salt-Stressed (NP-S, ○), Primed+Salt Stressed (P-S, ◇), n=8.

The Non-Primed Stressed (NP-S) and NaCl-Primed Stressed (P-S) lines represent seeds subjected to salinity stress. Both stressed conditions displayed significantly lower germination rates compared to their non-stressed counterparts, indicating that salinity stress negatively impacts seed germination. Seed priming, a pre-treatment process designed to enhance seed performance during germination, demonstrated positive effects in the stressed groups, which reached a germination rate of 36%. This suggests that priming likely activates protective mechanisms within the seeds, allowing them to respond more efficiently to even unfavorable conditions.

Seed priming not only benefits overall germination percentages but also accelerates the germination process. While salinity stress diminishes these benefits, primed seeds (P-S) maintained an advantage over the non-primed stressed seeds (NP-S) throughout the germination period.

Table 3.1. The effects of salt stress on germination parameters of primed (P) and non-primed (NP) seeds. $\pm$ represents standard error either side of the mean (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$).

<i>NaCl Salinity (mM)</i>	<i>NaCl Priming</i>	<i>Total Germination (%)</i>	<i>Mean Grmn. Time (days)</i>	<i>Germination Index</i>
0	NP	94.50 $\pm$ 1.99 a	4.37 $\pm$ 0.08 b	5.57 $\pm$ 0.13 a
	P	94.00 $\pm$ 1.30 a	4.26 $\pm$ 0.07 b	5.81 $\pm$ 0.11 a
150	NP	20.50 $\pm$ 4.30 c	7.85 $\pm$ 0.28 a	0.67 $\pm$ 0.14 c
	P	36.00 $\pm$ 4.79 b	7.37 $\pm$ 0.22 a	1.26 $\pm$ 0.17 b

NaCl salinity stress significantly decreased total germination rate and germination index, and prolonged mean germination time (Table 3.1). Although seed priming showed no difference under normal conditions, it significantly increased total germination rate by 15.5% and germination index by 0.6. Seed priming decreased mean germination time in both salinity levels compared to non-primed seeds; however, the difference was not statistically significant. Our findings demonstrate that NaCl stress inhibited germination in melon seeds. However, priming the seeds with NaCl enhanced their tolerance to salt stress by increasing germination rates in stressed seeds. These results are further supported by prior research on NaCl-priming in melon, rice, and sorghum (Xiaofei Chen *et al.*, 2021a; Sen & Puthur, 2020; N. Sivritepe *et al.*, 2003).

3.2. MIC Assay for Bacterial Salt Tolerance

All bacterial strains tested exhibited measurable growth across the varying NaCl concentrations (Figure 3.2). At a concentration of 6% NaCl, most strains displayed relatively high optical density (OD) values, with strains M8 and PR9 demonstrating the highest growth. As the NaCl concentration increased to 8% and then 10%, a general decline in OD values was observed for all strains, suggesting a reduction in bacterial growth at higher salinity levels. Strain M8 consistently exhibited the highest OD values across all NaCl concentrations, indicating a superior tolerance to salt stress compared to the other strains. Conversely, strain PR10 showed significantly lower OD values at each concentration point, suggesting a lower tolerance for salinity. Based on the observed growth patterns and potential for salt tolerance, strains PR9, M8, X4, X5, and PR8 were selected for further investigation.

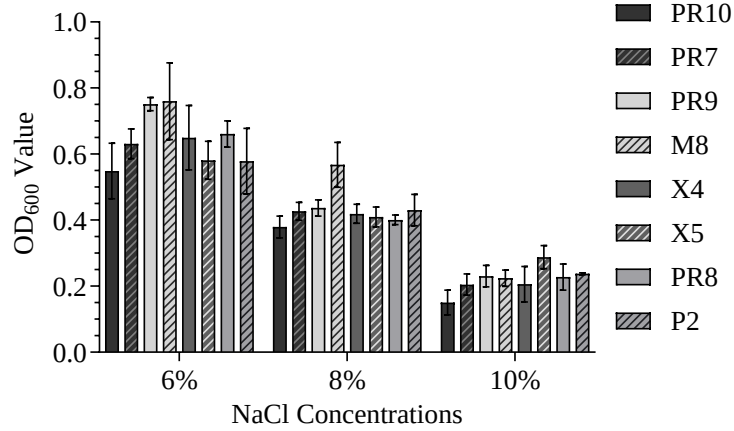


Figure 3.2. The growth of different bacterial strains (PR10, PR7, etc.) in terms of the optical density (OD) values at 600 nm in a medium containing increasing concentrations of NaCl (6%, 8%, 10%), n=3.

3.3. Pot Experiment and Growth Conditions

3.3.1. Field Capacity Determination

$$FC = M_2 - M_1 \quad (3.13)$$

where:

M₁: Dry weight of the pot containing the soil mixture (g)

M₂: Weight of the pot containing the soil mixture after 48 hours of saturation (g)

$$FC = 3000 \text{ g} - 2100 \text{ g} \quad (3.14)$$

$$FC = 900 \text{ g} \quad (3.15)$$

$$55\% FC = 500 \text{ g} \quad (3.16)$$

The initial dry weight of the pots was a total of 2100 grams, comprised the weight of the pot itself (100 grams) and the weight of the soil content (2000 grams). Following saturation and a two-day drainage period, the weight of the pots increased to 3000 grams. To quantify the soil's water-holding capacity, the weight of the absorbed water was determined by subtracting the initial dry weight from the saturated weight (Eq. 3.14). This value of 900 grams represents the amount of water the soil can hold at its field capacity, which is the point where all readily available water is held in the soil pores.

For subsequent irrigation treatments, the pots were subjected to 55% of the field capacity (FC), which translates to 500 grams of water per pot (Eq. 3.16). This brings the final weight of a pot to 2600 grams at the end of each irrigation cycle (2000 grams soil + 100 grams pot + 500 grams water).

3.3.2. Evapotranspiration Measurement

By day 5 of salinity stress, stressed plants showed significantly decreased evapotranspiration compared to controls (Figure 3.3). Treatments P, B, and PB displayed a trend towards higher water loss under salt stress, though not statistically different. The reducing effect of salinity in cumulative evapotranspiration agrees with Huang *et al.* (2012), who observed the effects of saline irrigation water on a local melon cultivar.

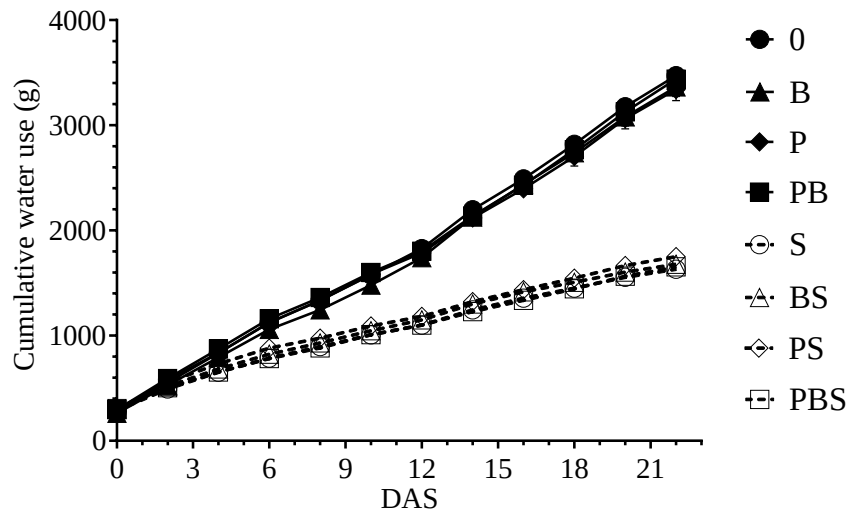


Figure 3.3. Time course of evapotranspiration (g) measured by daily weight loss of pots. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), n=8.

3.4. Plant Growth and Physiological Parameters

3.4.1. Plant Morphological Parameters

Stem length exhibited significant variation among treatment groups (Figure 3.4a). Contrary to our initial hypothesis, the control group (0) displayed the highest average stem length, near 70 cm. Salt-stressed groups, on the other hand, demonstrated statistically similar stem lengths, all being significantly shorter compared to the non-stressed treatments. These observations suggest that salt stress inhibits stem elongation in melon plants, warranting further investigation into the underlying physiological mechanisms.

Leaf numbers remained relatively consistent across most non-stressed treatment groups, with no statistically significant differences observed (Figure 3.4b). However, all salt-stressed groups exhibited a statistically lower number of leaves compared to their non-stressed counterparts. Interestingly, Group P under salt stress displayed a statistically higher number of leaves compared to the other stressed groups. This unexpected finding

necessitates further exploration to understand the specific interaction between salt stress and treatment P on leaf production.

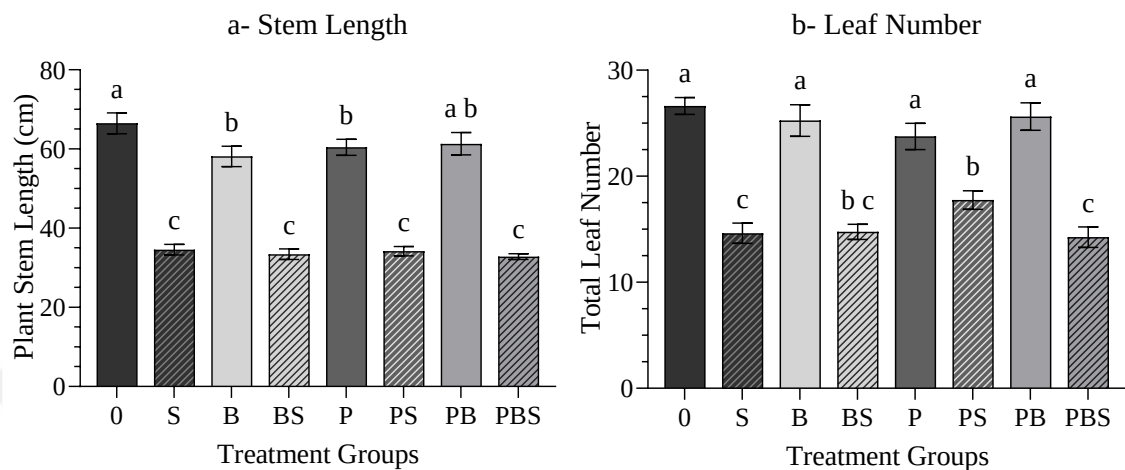


Figure 3.4. Final plant stem lengths (a) and leaf numbers (b) of melon plants at harvest (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$). Control (0), PGPB (B), NaCl-Priming (P), Priming+PGPB (PB), Salt (S), PGPB+Salt (BS), Priming+Salt (PS), Priming+PGPB+Salt (PBS), n=8.

Both stem length and leaf number are crucial factors influencing plant productivity and yield. Optimizing treatments based on their impact on these parameters has the potential to significantly enhance agricultural practices for melon cultivation. The observed complex effects of treatments on stem length and the unexpected response of leaf number under salt stress highlight the importance of tailored approaches for maximizing melon plant growth. Future research endeavors could delve deeper into the underlying mechanisms driving these treatment effects, providing valuable knowledge for further refinement of cultivation strategies.

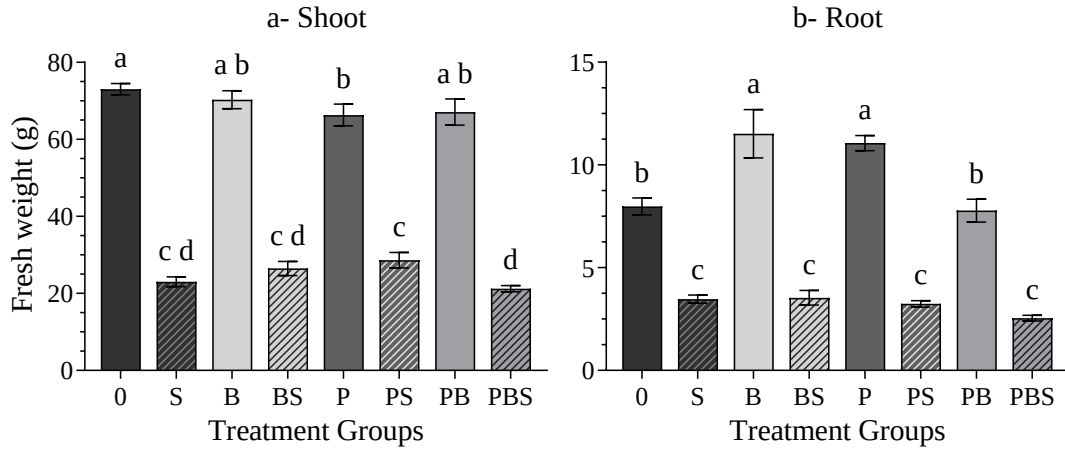


Figure 3.5. Shoot (a) and root (b) fresh weights of melon plants after harvest (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$). Control (0), PGPB (B), NaCl-Priming (P), Priming+PGPB (PB), Salt (S), PGPB+Salt (BS), Priming+Salt (PS), Priming+PGPB+Salt (PBS), n=8.

Salt stress significantly reduced shoot weight across all treatments, with neither priming nor PGPB inoculation mitigating this effect (Figure 3.5a). However, both treatments significantly increased root weight under non-stress conditions (Figure 3.5b). These findings align with previous research demonstrating that NaCl stress inhibits shoot and root fresh weight in tomato plants (Cordero *et al.*, 2018). Similarly, a separate study investigating three PGPB strains in wheat reported a positive effect on root weight but no significant contribution to seedling weight (Nawaz *et al.*, 2020). Besides, another study found NaCl-priming to be somewhat effective in increasing shoot and root fresh weight of sorghum plants (Xiaofei Chen *et al.*, 2021b).

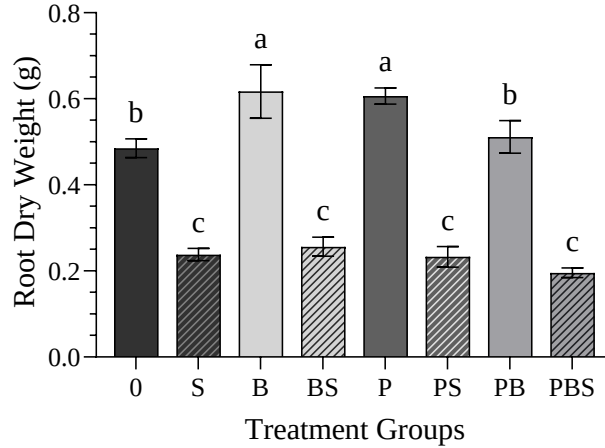


Figure 3.6. Root dry weights of melon plants after harvest (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$). Control (0), PGPB (B), NaCl-Priming (P), Priming+PGPB (PB), Salt (S), PGPB+Salt (BS), Priming+Salt (PS), Priming+PGPB+Salt (PBS), n=8.

In non-stressed conditions, bacterial inoculation (B) and seed priming (P) treatments resulted in a significant increase in dry root weight compared to the control group (0) and the combined application group (PB) (Figure 3.6). However, under salt stress, all treatment groups exhibited a decrease in root dry weight compared to non-stressed conditions. Interestingly, no statistically significant differences in dry root weight were observed among the application groups (0, P, B, PB) under salt stress.

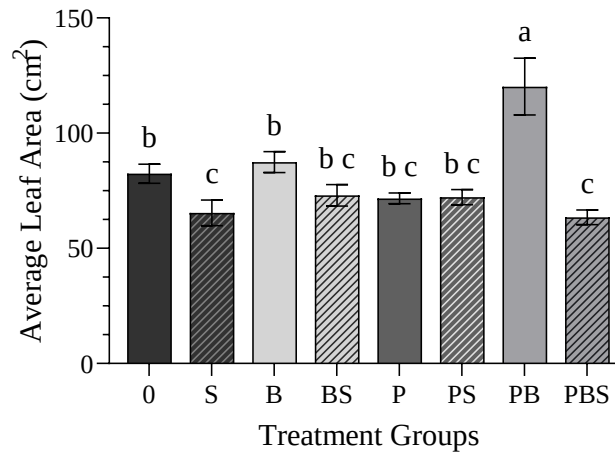


Figure 3.7. Average leaf areas (cm²) of uppermost 3rd leaves of melon plants after harvest (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$). Control (0), PGPB (B), NaCl-Priming (P), Priming+PGPB (PB), Salt (S), PGPB+Salt (BS), Priming+Salt (PS), Priming+PGPB+Salt (PBS), n=8.

The findings regarding leaf area in Figure 3.7 present an interesting interplay between salt stress, seed priming, and PGPB application. As expected, the combined treatment group

(priming + PGPB, PB) displayed the highest average leaf area, suggesting a potential synergistic benefit for leaf growth under non-stressed conditions. This could be due to the combined effects of priming-induced stress tolerance and PGPB-mediated growth promotion. Control (0) and bacteria (B) treatments show similarly high leaf areas (labeled 'b') and no significant difference between them. The stressed groups with control (S) and combined treatment (PBS) have the lowest leaf areas (labeled 'c') and are significantly different from all other groups. Although salt stress was expected to reduce leaf area, the data reveals a more nuanced pattern. While the control (S) and combined treatment (PBS) groups under salt stress did exhibit the expected decrease, the other stressed groups (BS and PS) did not show a statistically significant difference in leaf area compared to the non-stressed groups (B and P).

3.4.2. Relative Membrane Permeability (RMP) Assay

The analysis of relative membrane permeability (RMP) following salt stress exposure revealed intriguing patterns across the treatment groups (Figure 3.8). Increased membrane permeability is generally associated with cellular stress and damage. The priming groups (P and PB), both with and without PGPB application, displayed the lowest RMP values, indicating the least membrane damage.

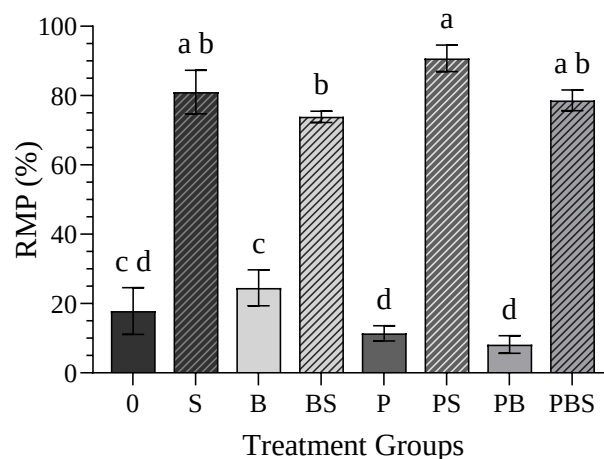


Figure 3.8. Relative membrane permeability (%) of melon plants after harvest (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$). Control (0), PGPB (B), NaCl-Priming (P), Priming+PGPB (PB), Salt (S), PGPB+Salt (BS), Priming+Salt (PS), Priming+PGPB+Salt (PBS), n=8.

This suggests that priming potentially enhanced membrane stability and mitigated the negative effects of salt stress on cellular integrity. As expected, salt stress caused an

increase in membrane permeability across all groups. In contrast to the unstressed priming (P) application, the highest RMP value was observed in the stressed priming (PS) application, indicating that the membranes were most damaged in the PS group. Additionally, salt stress caused the least damage to the bacterial (BS) group with the lowest RMP values among the unstressed groups, suggesting some level of protection from PGPB application.

3.4.3. Relative Water Content (RWC) Assay

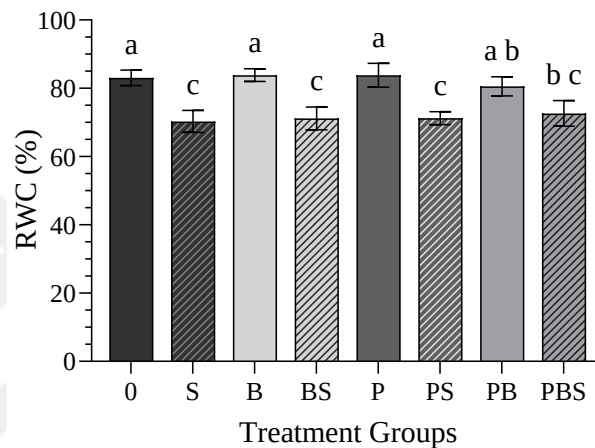


Figure 3.9. Relative water content (%) of melon plants after harvest (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$). Control (0), PGPB (B), NaCl-Priming (P), Priming+PGPB (PB), Salt (S), PGPB+Salt (BS), Priming+Salt (PS), Priming+PGPB+Salt (PBS), n=8.

Figure 3.9 illustrates the relative water content (RWC) percentage of melon plants after harvest. Although remedial applications were anticipated to increase the RWC percentage under both unstressed and stressed conditions compared to the control groups, no statistical difference was found within the stressed and unstressed groups. However, as expected, salt stress reduced the RWC percentage across all application groups, likely due to osmotic and ionic imbalances that impair water uptake and retention.

3.5. Plant Photosynthetic Measurements

3.5.1. Dark-Adapted Chlorophyll Fluorescence

Chlorophyll fluorescence measurements commenced on the initiation date of the salt stress treatment. This initial measurement was conducted prior to the application of salt solution to the designated salt stress groups, identified by the letter "S" in their labels (refer to Figure 2.2). Subsequent measurements were taken on 3 days after salt stress (DAS), 7

DAS, 11 DAS, 16 DAS, 18 DAS, 20 DAS, and 22 DAS. The data collected over these 8 days were then plotted on a logarithmic timescale, as shown in the OJIP curves presented below Figure 3.10.

The OJIP (O-J-I-P) curve reflects the characteristic rise in chlorophyll *a* (Chl *a*) fluorescence in response to increasing irradiance. This rise corresponds to the progressive reduction of the primary quinone electron acceptor (Q_A) in Photosystem II (PSII) prior to its re-oxidation by Photosystem I (PSI) (R. J. Strasser *et al.*, 2004). As the curve rises, it indicates an increase in the light energy used for Q_A reduction and the number of PSII reaction centers occupied by reduced Q_A (R. J. Strasser *et al.*, 2004).

PSII can be functionally divided into the donor side and the acceptor side. The primary electron donor in PSII is P680, a reaction center chlorophyll dimer that becomes oxidized ($P680^+$) upon the giving of an excited electron via light to the PSII primary acceptor pheophytin (Pheo). The oxygen-evolving complex (OEC) on the donor side recovers $P680^+$ through splitting water molecules (H_2O) (Blankenship, 2002). The excited electron from $P680^+$ is then transferred through a series of acceptors: pheophytin (Pheo), Q_A , and Q_B , ultimately reaching the plastoquinone (PQ) pool, where PQ is reduced to plastohydroquinone (PQH_2) as the terminal acceptor (Blankenship, 2002).

The OJIP curve provides a time-resolved view of electron movement through PSII as light intensity increases. While a perfect one-to-one correspondence between specific curve features and PSII steps cannot be established, the prominent K-step at approximately 0.3 milliseconds (ms) and the J-step at around 2 ms are generally attributed to events on the donor side (R. J. Strasser *et al.*, 2004). Conversely, the I-P phase is likely associated with electron transfer processes on the acceptor side of PSII. Additional parameters derived from the OJIP curve, such as the F_v/F_m ratio, ABS/RC , and Et_o/RC , offer a more comprehensive assessment of PSII functionality (Mehta, Jajoo, Mathur, & Bharti, 2010). A two-way ANOVA revealed a significant interaction ($p < 0.001$) between time (light duration) and treatment effects on OJIP fluorescence values, except for 11 DAS. This interaction effect complicates the interpretation of the main effects of treatments solely based on p-values and F-values. The significant interaction signifies that the fluorescence response of any treatment might change dynamically over time, making it challenging to discern the overall treatment effect.

The absence of a significant interaction on 11 DAS suggests a potential stabilization phase in response to salt stress, where the time (light duration) effect becomes the dominant factor. Overall, the data confirms that both the duration of salt stress and the specific treatments significantly impact plant physiological responses, as reflected by the variations in the OJIP curves (Figure 3.10). Furthermore, the interaction between these factors is intricate and exhibits temporal variation, highlighting the dynamic and treatment-specific nature of plant stress responses. An interesting observation is the increase in the total variation attributable to the interaction between time and treatments from 0.73% before stress to 9% on the final day. Conversely, the total variation due to time decreased by 17.8%, while the variation due to treatments increased by 8.4%. This rise in inter-treatment variations explains the progressive divergence observed in the fluorescence curves over time.

Analysis of the O-step (at 0.03 ms), representing the minimum fluorescence yield (F_o) of PSII, revealed no significant differences between treatments across all measurement days. The F_o value reflects the basal fluorescence emitted when all PSII reaction centers are in the open state, signifying the absence of electron transfer. Consequently, it serves as an indicator of the light-harvesting antenna complex (LHCII) health. The absence of a significant treatment effect on F_o , both before and after salt stress application, suggests that the applied stress level did not negatively impact the LHCII in our experiment (Mathur, Jajoo, Mehta, & Bharti, 2011). These antenna complexes are responsible for capturing light and directing the excitation energy towards the PSII reaction center.

In contrast, studies have reported a decrease in F_o values in wheat leaves exposed to increasing salt concentrations (0.1 M to 1 M) (Mehta, Allakhverdiev, & Jajoo, 2010; Mehta, Jajoo, *et al.*, 2010). Mehta *et al.* (2010) concluded that salt stress primarily damaged the donor side of PSII in wheat leaves, and this damage was irreversible compared to the acceptor side. Conversely, our results with melon suggest that salt stress-induced damage may be partly reversible with the application of proper irrigation practices, as evidenced by the lack of F_o decline across treatment groups throughout the experiment. The observed disparity between our findings and those reported for wheat might be attributed to the inherent differences in salt tolerance between the two plant species. While melon exhibits partial salt tolerance (Akrami & Arzani, 2019), wheat

varieties are generally considered more sensitive to salt stress (El Sabagh *et al.*, 2021). This inherent difference in salt tolerance likely explains the observed variation in response to salt stress between the two plant species.

Eight treatment groups exhibited statistically significant differences at some points within the first 7 DAS. Notably, the control and salt stress groups did not show any clear distinction until this timeframe. On the 7th day, a downward fluctuation was observed in the groups subjected to salt stress (hollow symbols, Figure 3.10). This fluctuation in the O-P phases began to appear at approximately 0.3 ms, corresponding to the K-step previously observed under various stress conditions like heat and drought (Guissé, Srivastava, & Strasser, 1995; Lazár & Ilík, 1997; Srivastava, Guissé, Greppin, & Strasser, 1997). Heat stress resulted in a decrease followed by a rapid increase in the K-step towards the P-step (R. J. Strasser *et al.*, 2004), like the response to salt stress depicted in Figure 3.10 for 7 DAS. The K-step is typically 'concealed' within the O-J rise because of the established equilibrium among the fluorescence increase reactions (R. J. Strasser *et al.*, 2004). Consequently, the appearance of the K-step is considered to result from a disruption of this normally established balance (Srivastava *et al.*, 1997). Extensive research (Guissé *et al.*, 1995; Srivastava *et al.*, 1997; B. Strasser, 1997) suggests that the K-step originates from the inactivation of the OEC, resulting in an electron flow imbalance within PSII. This supports the inference of Schreiber *et al.* (1995) on the most sensitive components of PSII being primarily associated with the PSII donor side, particularly the water-splitting site. OEC constitutes the rate-limiting step because while its inactivation may initially appear to accelerate electron flow, the electron pool is rapidly depleted (R. J. Strasser *et al.*, 2004).

Consistent with previous observations, the maximum fluorescence (F_m) values measured at the P-step (at 1000 ms) were lower in the salt stress groups compared to the control groups on day 7 DAS (Figure 3.10). However, this decline was less pronounced than the reductions observed during the O-I steps. This observation suggests a decline in photosynthetic efficiency and potential damage to the photosynthetic apparatus, particularly PSII. This phenomenon is linked to the inactivation of the OEC, diminished light energy capture in PSII, and impaired functionality of the electron transport chain, especially under extended salt stress conditions. The cumulative impact of these stressors

on PSII function ultimately manifests as a decline in the maximum fluorescence observed in the OJIP transient. Research on various plant species has consistently shown that salt stress leads to a reduction in F_m . Studies on sweet pepper cultivars (Giorio & Sellami, 2021) and lettuce seedlings (Shin *et al.*, 2020) revealed that higher saline concentrations significantly reduce F_m . These findings align with our own observations, further solidifying the detrimental effects of salt stress on F_m . This decrease in F_m highlights the compromised functionality of PSII likely due to salinity-induced physiological changes in plants.

By 11 DAS, (Figure 3.10), the statistically significant differences observed earlier had disappeared. Additionally, the fluctuations previously seen in the OJIP curves were no longer evident. The stabilization phase after salt stress is vital for plants' recovery and adaptation to challenging conditions. This period encompasses a range of physiological, biochemical, and molecular responses that enable the plant to adjust and sustain its metabolic functions. Initially, during salt stress exposure, plants encounter an osmotic phase that restricts the growth of young leaves due to decreased water uptake. This is followed by an ionic phase, characterized by the accumulation of excessive ions, particularly sodium and chloride, leading to cellular toxicity and oxidative stress. To counter these effects, plants activate several mechanisms, including ion homeostasis, osmotic adjustment, and detoxification pathways (Batool *et al.*, 2020; Muchate, Nikalje, Rajurkar, Suprasanna, & Nikam, 2016).

The OJIP curves for the salt stress groups revealed a downward trend beginning at the J-step, observed from 16 DAS (Figure 3.10) and persisting until the final day (Figure 3.10). Furthermore, the divergence between the salt stress groups (represented by hollow symbols) and the unstressed groups (represented by solid symbols) became progressively more pronounced as the duration of salt stress increased. This finding is particularly significant as the initial decrease on 7 DAS was confined to the K-step. The observed shift from the K-step to the J-step suggests a sequential progression of salt stress effects on the photosynthetic apparatus in plants. This progression suggests that the stress first disrupts the donor side of PSII (K-step), potentially affecting water oxidation. As the stress persists, the damage extends to the acceptor side (J-step), hindering electron transfer further downstream.

The observed decrease in the OJIP transient at the J-step (at 2 ms) signifies a further decline in electron transport chain efficiency. This step corresponds to the reduction of Q_A and the initiation of electron transfer to Q_B . A diminished J-step suggests a specific impairment in the ability of PSII to transfer electrons from Q_A to Q_B .

Our findings align with previous research on various plant species under salt stress. Studies have reported that the J-phase dip corresponds to a decrease in primary photochemical efficiency and an increase in non-photochemical quenching mechanisms (Xianjun Chen *et al.*, 2021; G. Wang, Chen, Hao, Li, & Liu, 2011). These adaptations represent the plant's attempt to dissipate excess light energy as heat and minimize damage to the photosynthetic apparatus. The presence of a J-step decrease in our study suggests a significant disruption in PSII function under salt stress, ultimately impacting overall photosynthetic performance and efficiency (Ceppi, Oukarroum, Çiçek, Strasser, & Schansker, 2012).

Importantly, no statistically significant differences were observed among the unstressed groups (represented by solid symbols) throughout the experiment, including the final day of observation. An interesting observation was made within the stress groups (represented by hollow symbols) on the last day of the experiment (Figure 3.11). While no statistically significant difference was detected between the control group (S) and the plant growth-promoting bacteria (PGPB) group (BS), the F_m values for these two groups were nonetheless higher compared to the priming (PS) and priming + bacteria (PBS) groups ($p = 0.003$). A reduction in maximum fluorescence yield (F_m) following seed priming under salt stress suggests a complex interaction between the initial physiological boost from priming and the subsequent stress caused by salinity. Seed priming, a pre-sowing treatment, aims to enhance germination and increase stress tolerance (Abdelhamid *et al.*, 2019). However, under salt stress conditions, the positive effects of priming might be partly negated by the adverse impacts of high salinity on photosynthetic efficiency and PSII stability. This decrease in F_m could be attributed to the production of proteolytic enzymes which degrade chlorophyll and damage photosynthetic machinery (Sabater & Rodriguez, 1978). While previous studies have shown that seed priming techniques often enhance chlorophyll fluorescence (Jisha & Puthur, 2016; Panuccio, Chaabani, Roula, & Muscolo, 2018), it was observed that, hydropriming might inadvertently reduce

chlorophyll content in certain wheat varieties, potentially compromising the photosynthetic machinery (Islam *et al.*, 2015).

Furthermore, the gap between the unstressed (represented by solid symbols) and stressed (represented by hollow symbols) groups at the P-step exhibits a gradual increase from the 16 DAS to the final day of the stress (Figure 3.10).



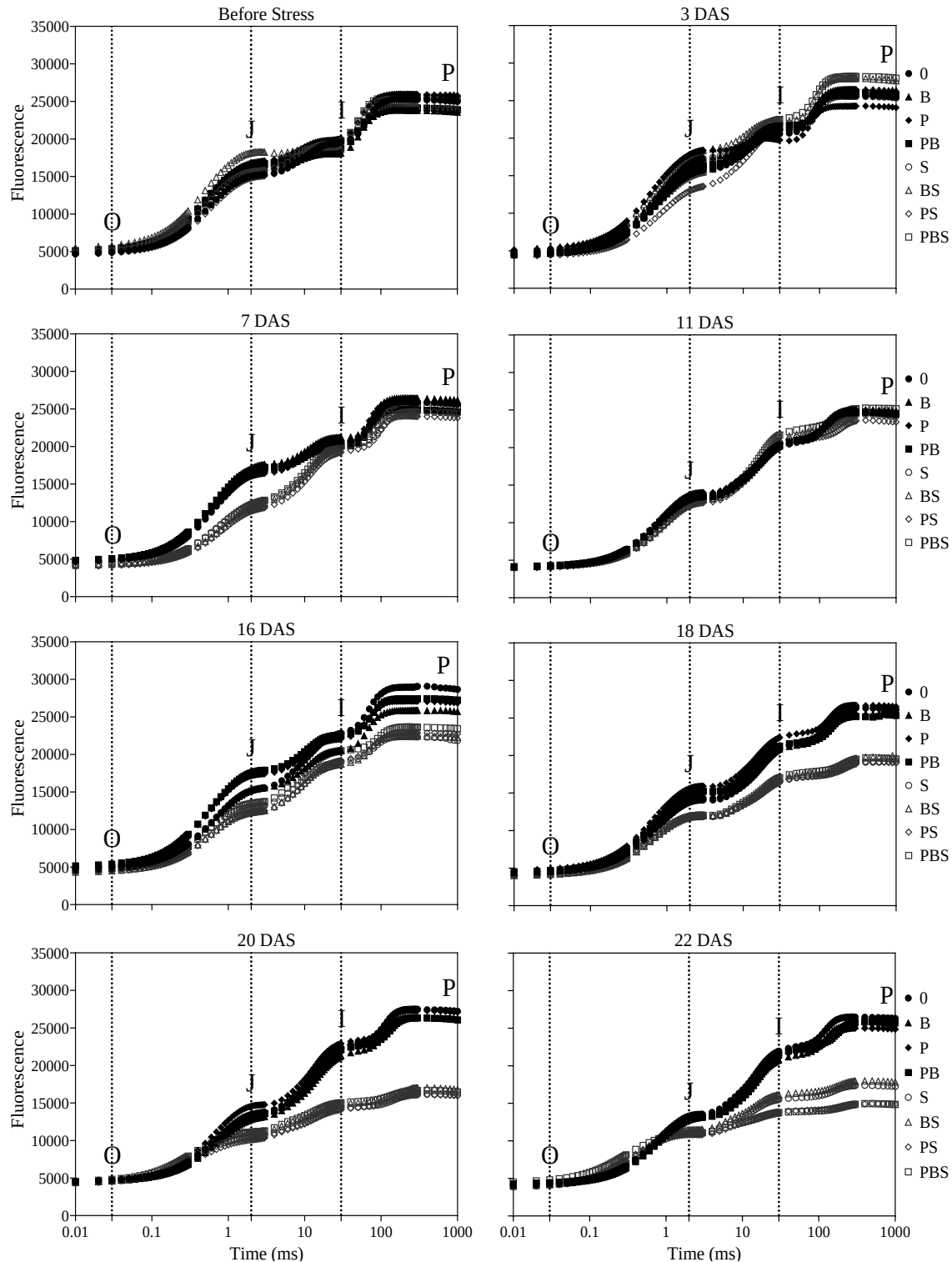


Figure 3.10. Average OJIP induction curves of melon plants subjected to different treatments measured at different time points: before stress, 3 days after stress (DAS), 7 DAS, 11 DAS, 16 DAS, 18 DAS, 20 DAS, and 22 DAS (n=8). Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □).

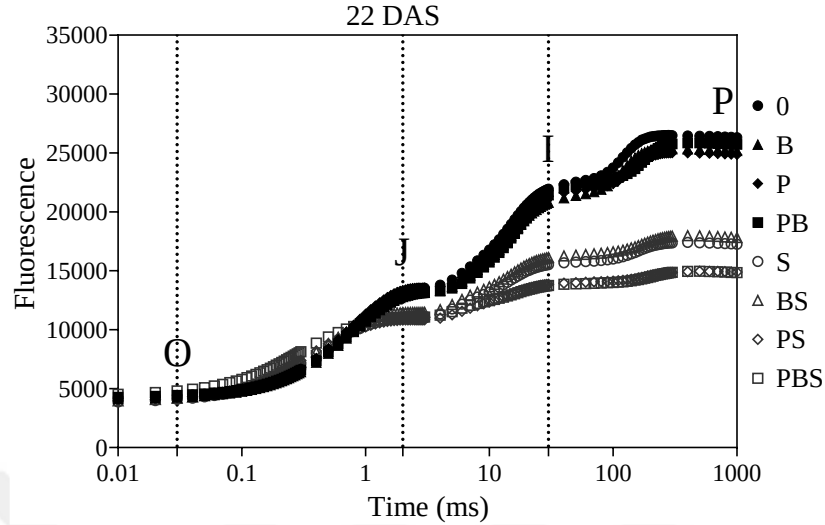


Figure 3.11. Average OJIP (O-J-I-P) induction curves for melon plants at the end of the experiment (December 22nd) subjected to different treatments (n=8). Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □).

We analyzed the time-course changes of several parameters derived from OJIP curves (Figures 3.12-3.15) to investigate the impact of salt stress duration on PSII function. These parameters, including maximum fluorescence yield (F_m , Figure 3.12), absorption efficiency per reaction center (ABS/RC, Figure 3.13), potential for primary photochemistry (Φ_{Po} , F_v/F_m Figure 3.14), and performance index based on light absorption (PI_{ABS} , Figure 3.15), were calculated as described in Section 2.6.1.

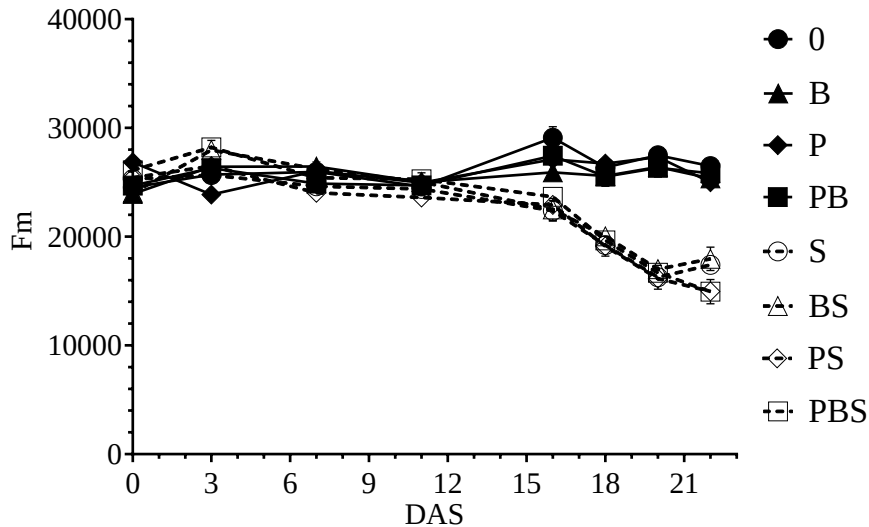


Figure 3.12. The time course of maximum fluorescence (F_m) of melon plants over a period of 22 days following the salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), n=8.

Our observations revealed a progressive decrease in Fm towards the end of the salt stress period (Figure 3.12). This decline suggests potential disruptions within the PSII electron transport chain, particularly affecting the efficiency of energy transfer between QA and QB. Several factors could contribute to this disruption, such as structural damage to PSII, reduced synthesis of essential proteins, or an accumulation of ROS. Consequently, the decrease in Fm reflects a decline in PSII's photochemical efficiency, hindering its ability to convert light energy into chemical energy. This ultimately translates to reduced photosynthetic performance, lower biomass production, and overall plant health degradation under stress conditions. Salt stress is known to disrupt PSII function by increasing ionic concentrations (Na^+ and Cl^-) within the plant. For instance, Luo, Shi, Song, & Li (2019) observed a decrease in Fm in *Corylus heterophylla* $\times$ *C. avellan* seedlings under salt stress, indicating impaired PSII function and overall photosynthetic performance. Our observations of a decline in Fm despite seed priming (PS) and priming+PGPB treatments (PBS) suggest that these interventions, while potentially beneficial for some physiological and photosynthetic parameters, may not fully protect the PSII apparatus under salt stress (Figure 3.12). This aligns with the findings of Ghassemi-Golezani, Hosseinzadeh-Mahootchi, & Farhangi-Abri (2020) who reported a similar persistence of Fm decline in safflower treated with salicylic and jasmonic acids despite their mitigating effects on other stress indicators. These results collectively suggest that even with stress-alleviating treatments, some degree of PSII damage might be unavoidable under prolonged salt stress conditions.

Figure 3.13 depicts the changes in ABS/RC values over time. For most treatments, ABS/RC starts low, dips slightly around 4-6 days after stress application, with no statistically significant difference between treatments. Following this dip, the stressed groups exhibit a gradual increase in ABS/RC values, with a significant rise observed between 18 and 22 days. The PBS treatment shows the most notable increase, with ABS/RC peaking sharply around 22 days. Conversely, the control (S) and PGPB (BS) treatments display the smallest increase under salt stress. Notably, the unstressed groups maintain relatively stable and low ABS/RC values throughout the experiment.

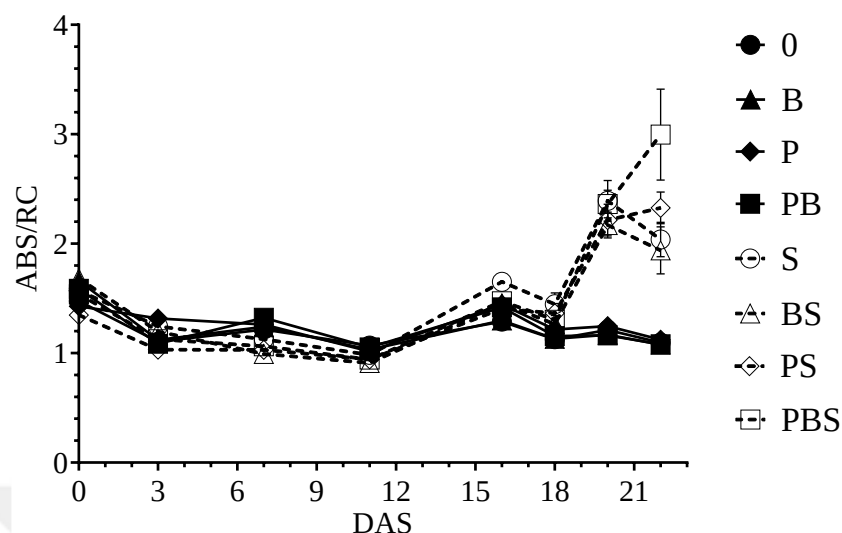


Figure 3.13. The time course of effective absorption flux per reaction center (ABS/RC) of melon plants over a period of 22 days following the salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), n=8.

ABS/RC indicates the average antenna size of PSII, representing the total light energy absorbed by PSII antenna pigments divided by the number of active reaction centers capable of reducing QA (Jajoo, 2013). The observed increase in ABS/RC is likely due to the inactivation of some active RCs under salt stress. Salt stress can directly damage PSII RCs, reducing their overall number and effectiveness (Kalaji *et al.*, 2016). This reduction increases the load on the remaining functional centers, which is reflected in the elevated ABS/RC value. Prolonged salt exposure can induce photoinhibition, where excessive light absorption overwhelms the processing capacity of PSII reaction centers (Hichem, El Naceur, & Mounir, 2009). A higher ABS/RC value indicates a decline in PSII efficiency, with a greater proportion of absorbed light energy not being efficiently used for photochemical processes, leading to increased heat dissipation or photodamage (Hichem *et al.*, 2009).

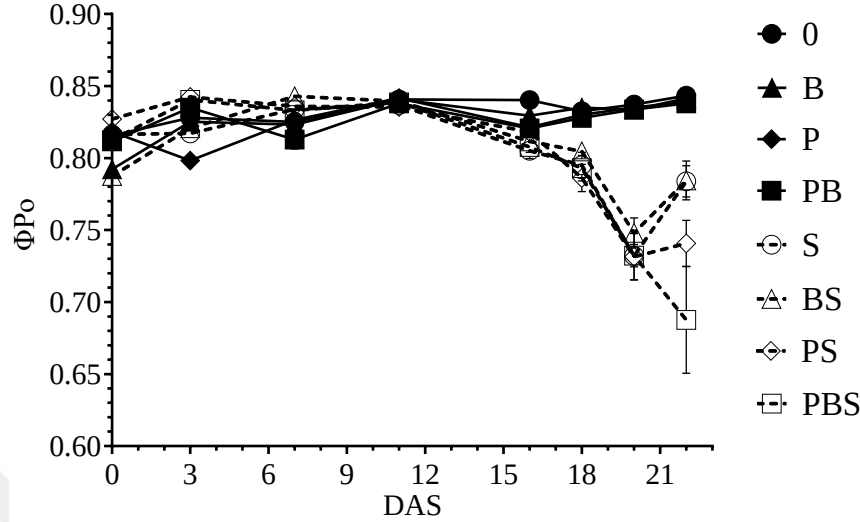


Figure 3.14. The time course of maximum quantum yield of PSII primary photochemistry (Φ_{Po} , F_v/F_m) of melon plants over a period of 22 days following the salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), $n=8$.

Figure 3.14 shows that Φ_{Po} values remain fairly stable across most treatment groups until about day 18, after which a notable decline is observed in the groups exposed to salt stress (S, BS, PS, PBS). Extended stress typically exacerbates the decline in F_v/F_m , indicating more severe damage to the photosynthetic machinery and reduced efficiency of PSII. Research investigating three wheat genotypes under drought stress revealed that F_v/F_m values only displayed a significant decrease on the final day of the drought period (Sommer, Han, Li, Rosenqvist, & Liu, 2023). This finding emphasizes the importance of stress duration, with prolonged stress leading to progressively greater reductions in PSII efficiency. A separate study examining the effects of increasing salt concentrations (0 to 200 mM NaCl) reported reductions in leaf area, shoot dry weight, and chlorophyll content (Bacarin, Falqueto, Moraes, Marini, & Löwe, 2007). However, the study did not identify any significant effects on F_v/F_m values. This suggests that short-term salt stress may not have an immediate impact on the maximum efficiency of PSII photochemistry.

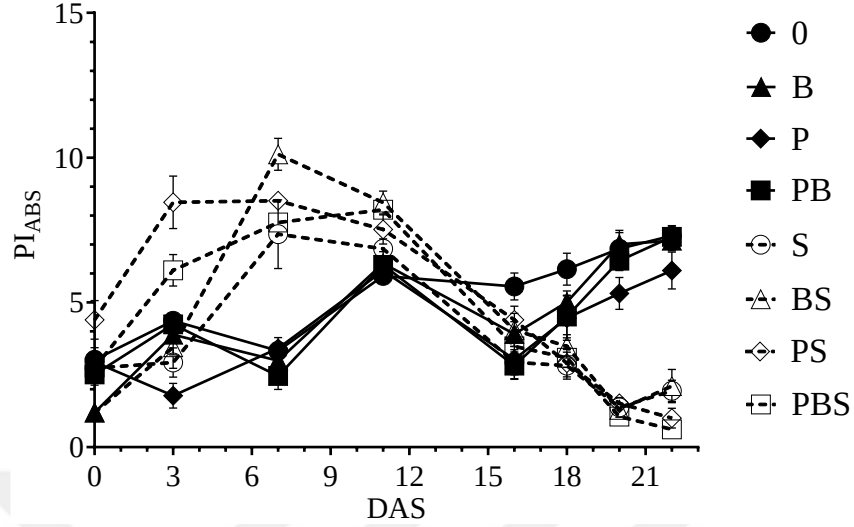


Figure 3.15. The time course of performance index on an absorption basis (PI_{ABS}) of melon plants over a period of 22 days following the salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), $n=8$.

Figure 3.15 depicts significant variations in performance index on an absorption basis PI_{ABS} values across treatment groups over time. Initially, all groups exhibit similar PI_{ABS} levels. However, by day 4, the salt-stressed groups (S, BS, PS, and PBS) display a rise in PI_{ABS} , peaking around day 8 before a sharp decline by day 12. Conversely, the unstressed groups (0, B, P, and PB) maintain relatively stable and higher PI_{ABS} values throughout the 22-day experiment.

PI_{ABS} is a composite metric derived from three independent parameters: the concentration of reaction centers per chlorophyll, which reflects the efficiency of capturing light energy by the photosynthetic apparatus; primary photochemistry, which gauges the initial conversion of light energy into excited electrons; and electron transport beyond Q_A , which evaluates the efficiency of transporting these excited electrons through the electron transport chain for ATP production (R. J. Strasser *et al.*, 2004). By integrating these aspects, PI_{ABS} offers a sensitive measure of potential disruptions across various stages of photosynthesis, including light harvesting, excitation energy trapping, and electron flow beyond Q_A (Kalaji *et al.*, 2016).

In a study of six sweet sorghum varieties exposed to 0-250 mM gradual salt stress, an increase in PI_{ABS} values was observed in some varieties compared to the control at 100

mM salt stress (Rastogi *et al.*, 2020). This increase may be related to the plants' activation of their defense mechanisms in response to initial salt stress. In our study, the increase in PI_{ABS} values between days 4-8 of salt stress suggests that the plants can resist stress through their defense mechanisms during the early stages of stress.

The following graphs show photosynthetic performance indicators derived from an analysis of the selected data in the OJIP curve at the end of the experiment (December 22nd). These indicators quantify the efficiency of Photosystem II (PSII) as described by the formulae in section 2.6.1 (R. J. Strasser *et al.*, 2004).

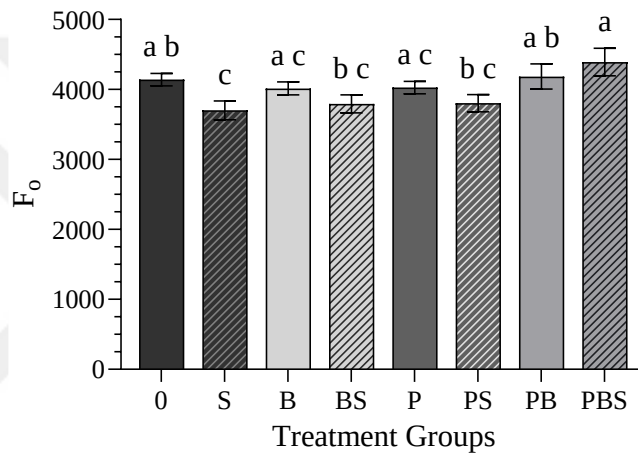


Figure 3.16. Minimum fluorescence (F_o) of melon plants on the last day of the experiment (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$).

As can be seen in the OJIP curves (Figure 3.10), there is little variation and statistically no significant difference (at $p < 0.001$) in the minimum fluorescence (F_o) values between the applications and between the stressed and unstressed groups. F_o represents the basal fluorescence level when all PSII reaction centers are open, indicating the absence of electron transfer. As such, it serves as an indicator of LHCII health, antenna complexes responsible for capturing light and channeling the excitation energy towards the PSII reaction centers. The observed lack of treatment effect on F_o , both before and after salt stress, suggests that the applied stress level did not negatively impact the LHCII in our melon experiment. Prior studies using wheat exposed to higher salt concentrations (Mehta, Allakhverdiev, *et al.*, 2010; Mehta, Jajoo, *et al.*, 2010) reported F_o reductions, suggesting irreversible damage to the PSII donor side. Conversely, consistent F_o levels in our melon experiment, despite salt stress, suggest potentially reversible damage with proper

irrigation. This difference might be due to the inherent salt tolerance variation between melon (Akrami & Arzani, 2019) and wheat (El Sabagh *et al.*, 2021).

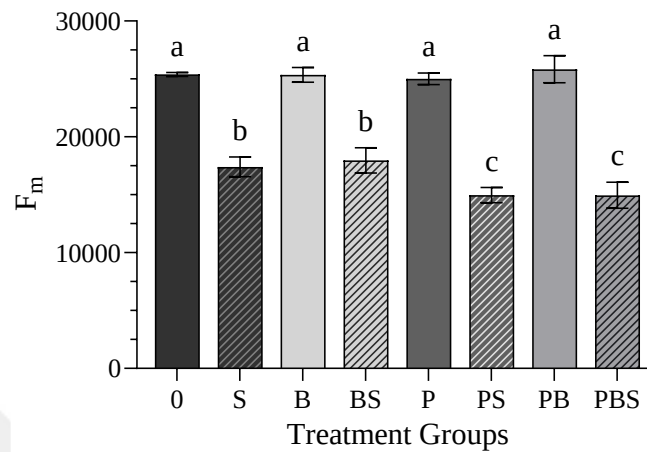
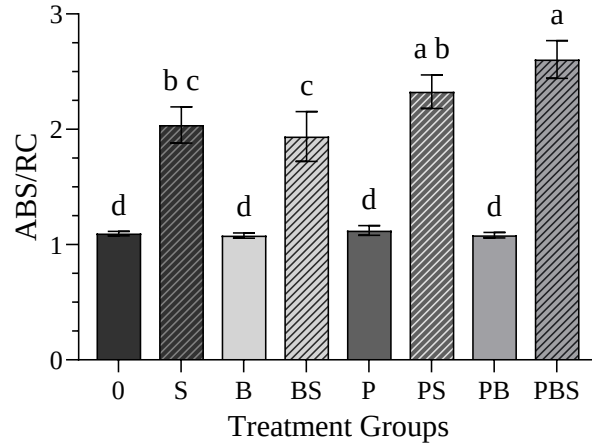


Figure 3.17. Maximum fluorescence (F_m) of melon plants on the last day of the experiment (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$)

Throughout the experiment, the F_m values in the unstressed groups (0, B, P, PB) remained stable and showed no statistically significant differences on the final day of observation (Figure 3.17). This stability indicates that plants not subjected to salt stress maintained healthy PSII function during the entire observation period. In contrast, an interesting pattern emerged within the stressed groups on the last day. Although there was no statistically significant difference in F_m values between the control group (S) and the PGPB group (BS), these values were higher than those observed in the primed (PS) and primed + bacteria (PBS) groups. This suggests that the application of PGPB might provide some level of protection against salt-induced PSII damage, despite the lack of a statistically significant difference compared to the control group. The decrease in F_m observed in the primed groups (PS and PBS) under salt stress points to a complex interaction between the initial physiological benefits of priming and the subsequent stress response. Seed priming, typically used to enhance germination and stress tolerance (Abdelhamid *et al.*, 2019), may be partially counteracted by the negative effects of high salinity on PSII function, as observed in our experiment. This is consistent with previous studies, such as (Islam *et al.*, 2015), which found that hydropriming reduced chlorophyll content in some wheat varieties, potentially compromising the photosynthetic machinery.



Further research is needed to clarify the specific mechanisms underlying the observed interaction between seed priming and salt stress on PSII function.

Figure 3.18. Effective absorption flux per reaction center (ABS/RC) of melon plants on the last day of the experiment (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$).

By the final day of salt stress, no statistical difference was observed in the absorption flux per reaction center (ABS/RC) values between the control groups (0, B, P, PB). However, when compared to the stress groups (S, BS, PS, PBS), the ABS/RC values in the control groups were statistically lower. The increase in ABS/RC is likely attributable to the inactivation of some active reaction centers (RCs) due to salt stress. Salt stress can directly damage PSII RCs, diminishing their overall number and efficiency (Kalaji *et al.*, 2016). This reduction places greater demand on the remaining functional centers, resulting in elevated ABS/RC values. Among the stress groups, seed priming alone (PS) and the combined treatment of seed priming with PGPB inoculation (PBS) showed statistically higher values, indicating that these treatments were not sufficient to fully protect the RCs from the damaging effects of salt stress.

Seed priming and PGPB inoculation are recognized for their ability to enhance plant stress tolerance by improving physiological and biochemical responses, such as antioxidant defenses, nutrient uptake, and photosynthetic efficiency (Abdelhamid *et al.*, 2019; Ghorbani *et al.*, 2018). While specific references may not directly address the negative synergistic effects of combining seed priming with PGPB inoculation, studies do highlight the differential impacts and complexities of plant-microbe interactions, which can sometimes result in adverse outcomes under certain conditions. For instance, a study on

chickpea found that seed priming with boron and inoculation with *Bacillus* sp. improved growth under boron deficiency. Nevertheless, higher boron concentrations proved toxic, reducing germination success (Mehboob *et al.*, 2022). It is important to note that this study did not examine the effects of co-application on the photosynthetic parameters of plants. In our experiment, while seed priming with a 0.9% NaCl solution alone improved seed germination parameters under salt stress, the addition of five *Bacillus* sp. strains appeared to have complex negative effects on PSII health in primed seeds. This study is the first to present evidence that a nonpathogenic associative bacterial consortium might inhibit the ameliorative effects of seed priming when co-applied.

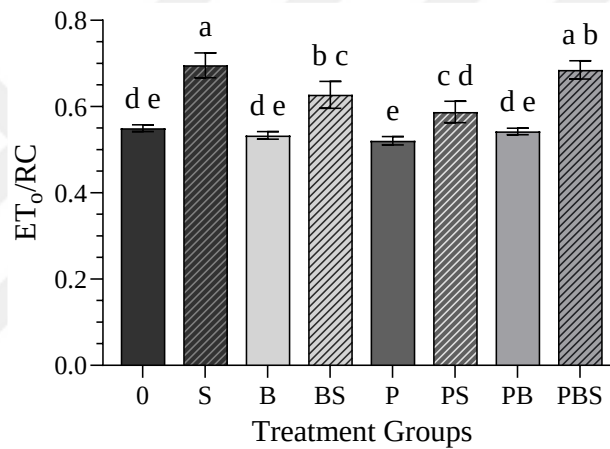


Figure 3.19. Electron transport rate (ETR) beyond plastoquinone-A (ET₀/RC) of melon plants on the last day of the experiment (n=8). Values not associated with same letters are significantly different ($p \leq 0.05$).

Figure 3.19, illustrating the electron transport rate beyond plastoquinone-A (ET₀/RC), shows significant variations among the different treatment groups. Unstressed groups exhibit lower ET₀/RC values, with the primed group (P) having the lowest. In contrast, the stressed control group displays the highest ET₀/RC, followed by the PBS group. The remaining stressed groups (BS, PS) show intermediate values. ET₀/RC reflects the electron transport rate per PSII reaction center. It represents the energy utilized by a single reaction center for electron transfer (Sun, Zhang, Gao, Shu, & Wang, 2009). Similar to the ABS/RC data, the increase in ET₀/RC within stressed groups likely reflects the inactivation of some PSII RCs due to salt stress. Elevated ET₀/RC values under salt stress suggest that stress primarily inhibits reaction centers rather than electron transfer within PSII (Yanhui *et al.*, 2020). Salt stress can directly damage PSII reaction centers, reducing

their overall number and efficiency (Kalaji *et al.*, 2016). This decrease in functional centers necessitates a higher workload for the remaining ones, leading to the observed increase in ETo/RC.

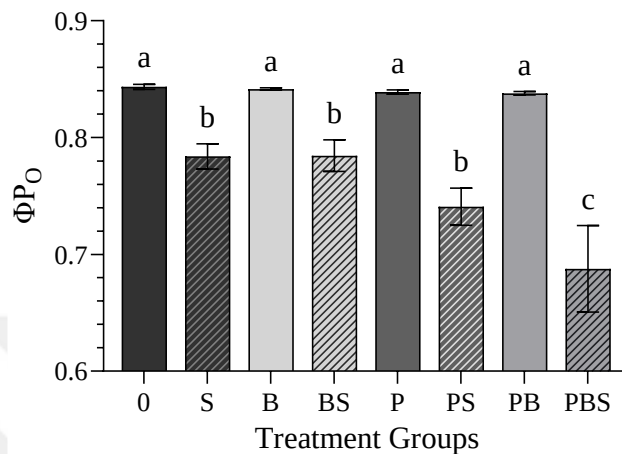


Figure 3.20. Maximum quantum yield of PSII primary photochemistry (Φ_{Po} , F_v/F_m) of melon plants on the last day of the experiment ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Figure 3.20 shows significant differences in the maximum quantum yield of PSII primary photochemistry (Φ_{Po}) among the various treatment groups. The control group (0), PGPB (B), Priming (P), and PB groups maintain high Φ_{Po} values, close to 0.85. The optimal quantum yield (Φ_{Po} , F_v/F_m) typically averages around 0.83 in the unstressed leaves of various species and ecotypes (Björkman & Demmig, 1987). This consistency indicates a fundamental similarity in the primary light-converting processes across different plant species (Schreiber *et al.*, 1995). The groups with salt stress (S, BS, PS, PBS) have lower Φ_{Po} values, with the PBS group showing the lowest Φ_{Po} , indicating a significant negative impact of the combined stress treatment. The fact that the combined application under salt stress has the lowest Φ_{Po} (or F_v/F_m) value confirms the negative synergistic effect observed in other fluorescence parameters.

Previous research suggests that certain plant genotypes can recognize specific PGPB as pathogens and develop immunity against them (Brusamarello-Santos *et al.*, 2019). In our study, applying PGPB in isolation did not exhibit any negative effects on photosynthetic parameters. However, seedlings grown from primed seeds displayed a clear inhibitory effect of PGPB on several fluorescence parameters. This unexpected observation may be attributed to potential indirect alterations in the plant's immune response mechanism

triggered by the seed priming process. Seed priming is known to induce various indirect changes within the plant's immune response system, enhancing its ability to withstand both biotic and abiotic stresses (Conrath, Beckers, Langenbach, & Jaskiewicz, 2015). Seed priming not only activates pre-germinative seed metabolism, leading to the induction of antioxidant systems and DNA repair pathways, but also alters secondary metabolism, resulting in the production of various defense metabolites (Q. Ali, Ashraf, Kamran, Rehman, & Ahmad, 2019). While the priming process is anticipated to enhance plant growth through an additive effect when combined with PGPB, the complexity of plant-bacteria interactions and their impact on the plant immune system appears to be multifaceted (Thomas-Vaslin, 2017), potentially transforming the expected additive effects into negative synergistic effects.

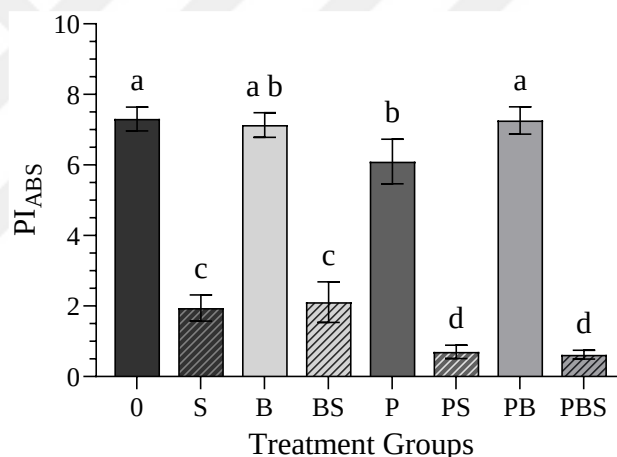


Figure 3.21. Performance index on an absorption basis (PI_{ABS}) of melon plants on the last day of the experiment ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Our experiment (Figure 3.21) reveals significant variations in PI_{ABS} values among treatment groups. The control and combined application (PB) groups display the highest PI_{ABS} , suggesting optimal photosynthetic performance. Plants in the B and P groups also maintain relatively high PI_{ABS} values. Conversely, salt-stressed groups (S, BS, PS, PBS) exhibit significantly lower PI_{ABS} , with PS and PBS showing the most pronounced decline. PI_{ABS} serves as a valuable tool for assessing the influence of environmental stressors (e.g., salinity, drought, extreme temperatures) on a plant's ability to capture and utilize light energy for photosynthesis (Kalaji *et al.*, 2016). A decrease in PI_{ABS} typically indicates a reduction in this efficiency. For instance, research investigating wheat under salt stress employed PI_{ABS} to evaluate the impact on photosynthetic performance (Ibrahimova *et al.*,

2021). The findings demonstrated a significant decline in PI_{ABS} under high salinity conditions, suggesting diminished PSII efficiency and overall photosynthetic capacity. Our study revealed an unexpected decrease in PI_{ABS} within the primed, unstressed (P) and stressed (PS) groups. Seed priming is generally thought to enhance overall seedling health. For instance, studies on waterlogged summer maize have shown that H_2O_2 priming can elevate PI_{ABS} and improve photochemical properties, ultimately leading to more efficient electron transport, photophosphorylation, and Calvin cycle activity (S. Wang *et al.*, 2022). However, research on other plant species, such as *Amaranthus tricolor* L., suggests that H_2O_2 priming can negatively impact photosynthesis by reducing seed quality and pigment levels (Gins, 2022). Interestingly, the decline in PI_{ABS} observed in the combined stress group (PBS) aligns with the trends seen in other chlorophyll fluorescence parameters, suggesting a potential link between these observations.

3.5.2. Gas Exchange and Light-Adapted Chlorophyll Fluorescence

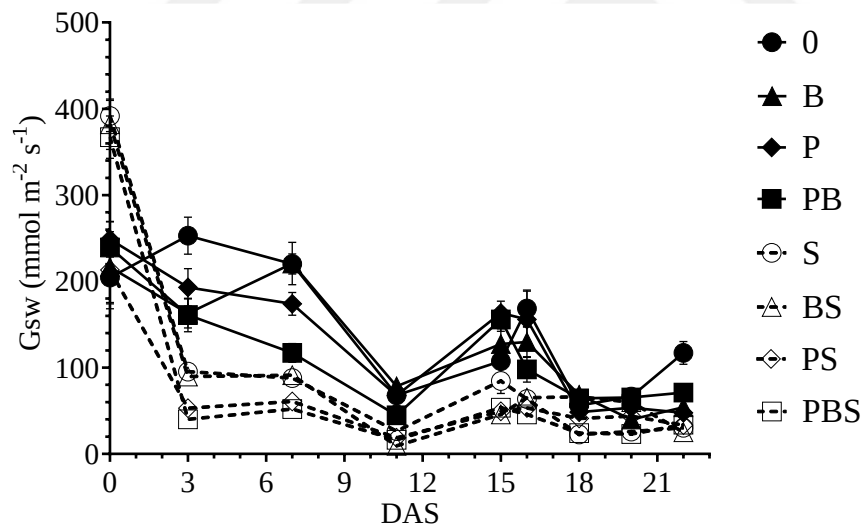


Figure 3.22. The time course of stomatal conductance to water vapor (G_{sw} , $mmol/m^2s$) in melon plants over a period of 22 days following the salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), $n=8$.

The time course of stomatal conductance to water vapor (G_{sw}) in Figure 3.22 reveals a sharp initial decline for all groups within the first few days. Control (0), PGPB (B), and seed priming + PGPB (PB) groups then maintain relatively higher G_{sw} values throughout the experiment compared to the other treatments. In contrast, the salt-stressed groups (S,

BS, PS, PBS) exhibit consistently lower G_{sw} values, indicating a more pronounced effect of salt stress on stomatal conductance.

This pattern suggests that salt stress progressively reduces stomatal conductance, potentially due to accumulating damage to the photosynthetic machinery. Lower G_{sw} values in stressed groups compared to controls likely reflect this. Stomatal conductance is a key factor influencing plant water-use efficiency and overall productivity under salt stress. This is because salt stress can significantly reduce photosynthetic capacity through limitations at both the stomatal and mesophyll levels (Volpe, Manzoni, Marani, & Katul, 2011).

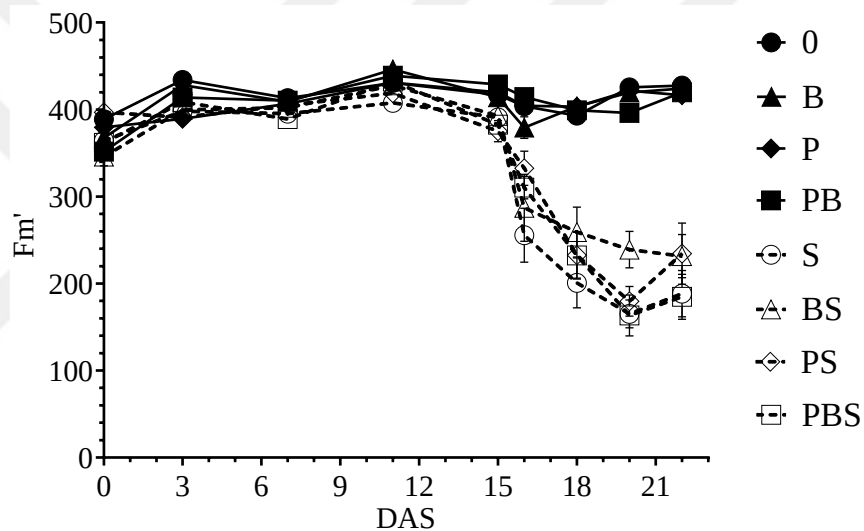


Figure 3.23. The time course of maximum light fluorescence (F_m') in melon plants over a period of 22 days following salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), $n=8$.

Light-adapted fluorescence is measured when the plant is exposed to light. This state reflects the actual functioning of photosystem II (PSII) under typical light conditions.

The time course of light fluorescence (F_m') reveals relatively stable values throughout the experiment for the control (0), PGPB (B), priming (P), and combined treatment (PB) groups (Figure 3.22). Conversely, the salt-stressed groups (S, BS, PS, PBS) exhibit a significant decrease in F_m' starting around 14 DAS, with the lowest values observed at the end of the observation period (22 DAS).

Maximum fluorescence yield under actinic light (F_m') signifies the efficiency of PSII in its active state. Unlike dark-adapted F_m measurements, F_m' accounts for PSII reaction

centers already involved in photochemistry. This makes Fm' a valuable tool for assessing a plant's real-time photosynthetic performance under ambient light conditions. By monitoring Fm', we gain insights into how a plant manages light energy and adapts to fluctuating light intensities or environmental stressors.

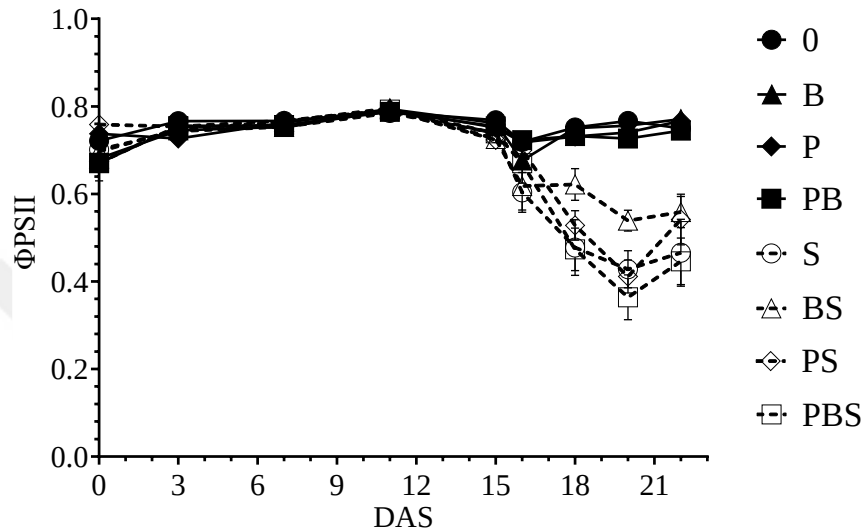


Figure 3.24. The time course of quantum efficiency in light (Φ_{PSII}) in melon plants over a period of 22 days following salt stress. Control (0, ●), PGPB (B, ▲), NaCl-Priming (P, ◆), Priming+PGPB (PB, ■), Salt (S, ○), PGPB+Salt (BS, △), Priming+Salt (PS, ◇), Priming+PGPB+Salt (PBS, □), $n=8$.

An analysis of the quantum efficiency of light (Φ_{PSII}) shows stable values throughout the experiment for the control (0), PGPB (B), priming (P), and combined treatment (PB) groups (Figure 3.24). In contrast, the salt-stressed groups (S, BS, PS, PBS) exhibit a decline in Φ_{PSII} starting around day 14, with the lowest values observed at the end of the experiment (20 DAS).

Φ_{PSII} , which represents the effective quantum yield of PSII, measures the efficiency of converting absorbed light into chemical energy during photosynthesis. Essentially, it indicates the proportion of light energy that is utilized for photochemical reactions under actual light conditions.

Salt stress disrupts Φ_{PSII} through various physiological and biochemical alterations that impair the photosynthetic apparatus. These disruptions include imbalances in water and ion homeostasis, leading to osmotic stress and ion toxicity that hinder the PSII electron transport chain. Additionally, salt stress can cause photoinhibition, a light-dependent

reduction in PSII's photosynthetic capacity due to damage to reaction centers or light-harvesting complexes, manifesting as lower Φ PSII due to less effective photochemistry.

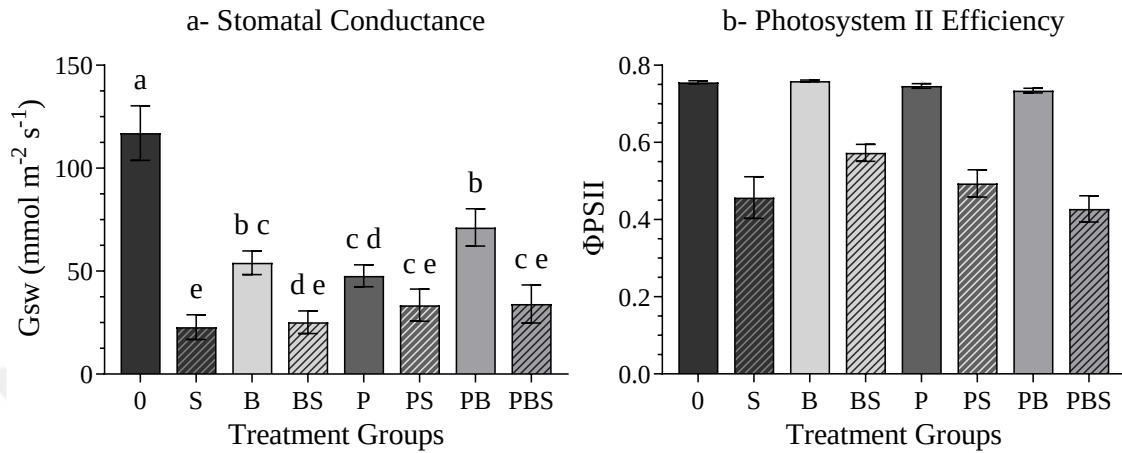


Figure 3.25. Stomatal conductance- G_{sw} (a) and photosystem II efficiency- Φ PSII (b) of melon plants prior to harvest ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Salinity stress significantly reduced G_{sw} in all groups except B (Figure 3.25a). Interestingly, individual treatments (P, B) decreased G_{sw} under control conditions, but trended higher under salt stress compared to the control and PB. Also, PGPB inoculation (B) had a stronger effect on G_{sw} than priming (P) under salt stress. Similarly, salinity stress reduced Φ PSII (Figure 3.25b). However, individual treatments displayed higher Φ PSII compared to the control and combined groups under salt stress. This indicates that both priming and PGPB inoculation potentially mitigated the negative effects of salinity stress on Φ PSII. These findings align with previous research on NaCl-priming in melon, where priming counteracted G_s reduction from salt stress (H. Ö. Sivritepe, Sivritepe, Eriş, & Turhan, 2005). Additionally, PGPB inoculation has been shown to increase G_s in melon under stress (Murgese *et al.*, 2020). Similarly, a separate study supports priming's protective effect on Φ PSII under salt stress, however, their finding of increased Φ PSII in non-stressed, primed plants was not replicated here. Inoculation with *Bacillus* also increased Φ PSII under stress, as reported elsewhere (Zhou *et al.*, 2022), supporting our findings.

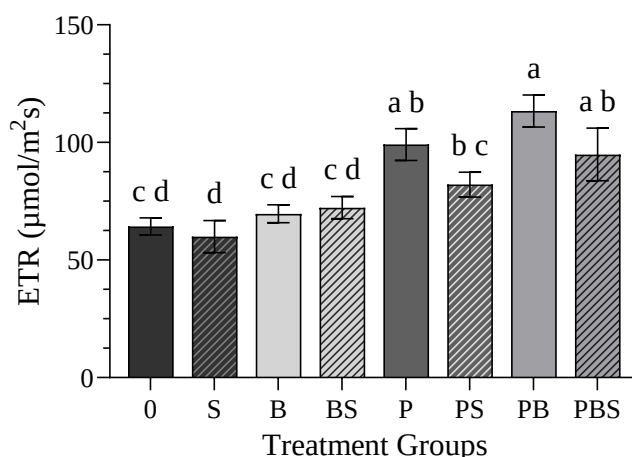


Figure 3.26. Electron transport rate (ETR, $\mu\text{mol}/\text{m}^2\text{s}$) of melon plants prior to harvest ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Analysis of the electron transport rate (ETR) in Figure 3.26 reveals significant variations among treatment groups (in $\mu\text{mol}/\text{m}^2\text{s}$). The control (0) and combined treatment (priming + PGPB, PB) groups exhibit the highest ETR values. In contrast, groups receiving only bacteria (B) or priming (P) treatments displayed ETR values closer to those of the salt-stressed groups. No statistically significant differences were observed between the stressed groups themselves.

ETR reflects the flow of electrons within the photosynthetic electron transport chain, primarily in Photosystem II (PSII) and Photosystem I (PSI). In essence, ETR provides insights into the overall activity of photosynthetic machinery and its ability to convert light energy into chemical energy. Stressful conditions like these can reduce ETR by either damaging the photosynthetic machinery or by causing stomatal closure, which limits the availability of CO_2 for photosynthesis.

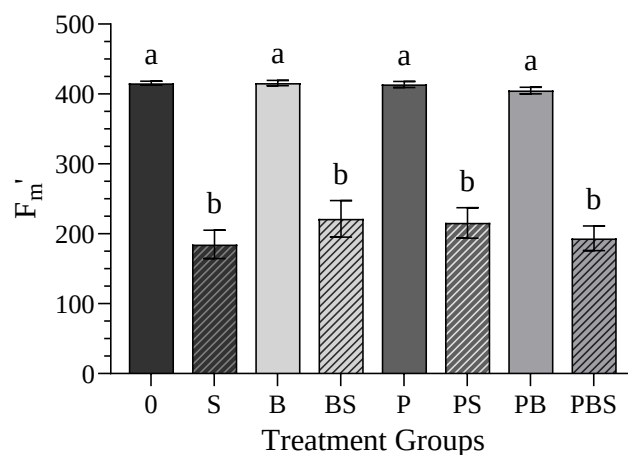


Figure 3.27. Maximum light fluorescence (F_m') of melon plants prior to harvest ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Salinity induced significantly pronounced ($\sim 50\%$) reductions in the fluorescence maximum in the light adapted state (F_m') of the melon seedlings (Figure 3.27). The F_m' was not significantly affected by bacterial inoculation or seed priming either in melon seedlings provided with saline or control irrigation. This would indicate that seed priming, and bacterial inoculation have little impact on the performance of PSII electron transport. However, the presence of salinity did impact the PSII electron chain, possibly indicating a lower capacity to emit excess radiation from the saturating light pulse as fluorescence. This would be supported by the OJIP responses of the melon seedlings presented in Figure 3.10 where salinity impairs electron transport through PSII.

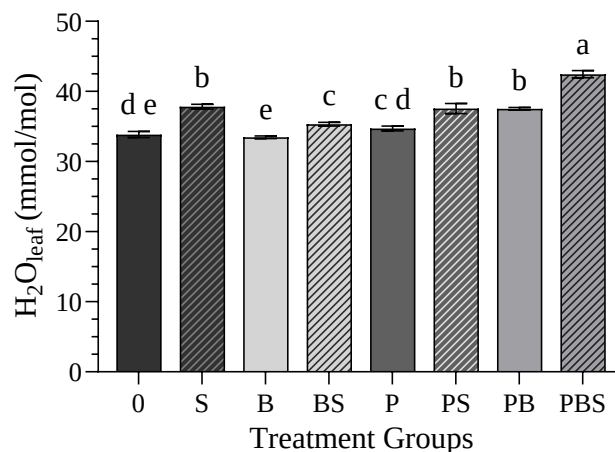


Figure 3.28. Leaf H_2O mole fraction ($H_{2O_{leaf}}$, mmol/mol) of melon plants prior to harvest ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Leaf water mole fraction (H_2O_{leaf}) is used to calculate leaf to air transpiration; therefore measurement of evapotranspiration and stomatal conductance confer greater insight into the ecophysiological status of the plant. Nonetheless, the results of the present study showed that melon seedlings exposed to salinity following bacterial inoculation had higher H_2O_{leaf} values than their control counterparts, this could indicate stomatal closure or enhanced loss of water vapor in the internal leaf airspace.

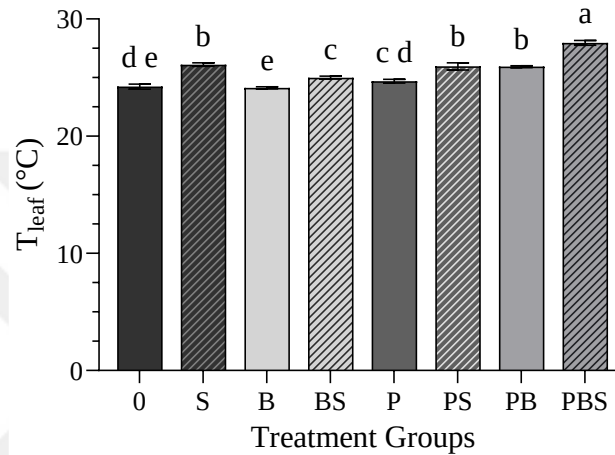


Figure 3.29. Leaf temperature (T_{leaf} , °C) of melon plants prior to harvest ($n=8$). Values not associated with same letters are significantly different ($p \leq 0.05$).

Leaf temperature (T_{leaf}) is a function of ambient temperature, incident radiation and convective cooling through leaf evapotranspiration. Variations in leaf temperature have been linked to stomatal conductance, whereby stomatal closure increases leaf temperature relative to ambient conditions (Jones, 1999b, 1999a). Values of T_{leaf} showed similar patterns to H_2O_{leaf} in that melon seedlings inoculated with bacteria and exposed to salinity exhibited higher temperatures than their control counterparts. Interestingly, salinity treatments did not induce a significant difference in T_{leaf} that could be associated with a salt stress induced reduction in stomatal conductance (Figure 3.25). Nevertheless, the lowest values of T_{leaf} were observed in the melon seedlings under control and bacterial inoculation with no exposure to salt stress.

4. CONCLUSION

This study examined the effects of salinity stress on melon plants and explored potential strategies to mitigate these effects. It was found that salinity significantly hindered various aspects of plant growth and development, such as germination, shoot and root growth, and photosynthesis. However, seed priming with a NaCl solution notably enhanced both germination and photosynthetic performance under saline conditions. Additionally, inoculating the plants with specific *Bacillus* strains further bolstered their resistance to salt stress.

The results suggest that seed priming with NaCl and *Bacillus* strain inoculation are effective strategies for alleviating salinity stress. However, the combined application of these methods did not produce a synergistic effect in this study. The study utilized a single salinity level, indicating the need for further research across a broader range of salinity concentrations. Investigating salinity levels typical of agricultural regions with high soil salinity, such as those in Euro-Mediterranean countries, would enhance the practical relevance of the findings. Additionally, extending the research to other commercially important plant species could expand the applicability of these strategies. Employing metabolomic and proteomic approaches may help elucidate the mechanisms underlying the beneficial effects of seed priming and *Bacillus* inoculation on seedling responses to salt stress.

The current study used a simple NaCl solution for seed priming. Future research could explore alternative priming methods, such as aerated priming or using different salt concentrations and osmolytes in the priming solution. While this study screened and used a mixture of five *Bacillus* strains, focusing on a smaller number of strains with the highest potential for stress mitigation in future studies could be beneficial. Furthermore, combinations of PGPB from different genera or contrasting natural environments might have varying effects on different crops' responses to a range of abiotic stresses. Investigating the impact of multiple inoculation episodes throughout the plant's growth cycle could also provide more sustained stress mitigation.

This experiment highlights the effectiveness of seed priming with a NaCl solution and *Bacillus* inoculation in mitigating the adverse effects of salinity on melon seedlings. These approaches could represent cost-effective, sustainable solutions for agriculture in saline-

affected areas where low-quality water is used for irrigation. Optimizing these techniques for combined application warrants further investigation to maximize their effectiveness for agricultural purposes.



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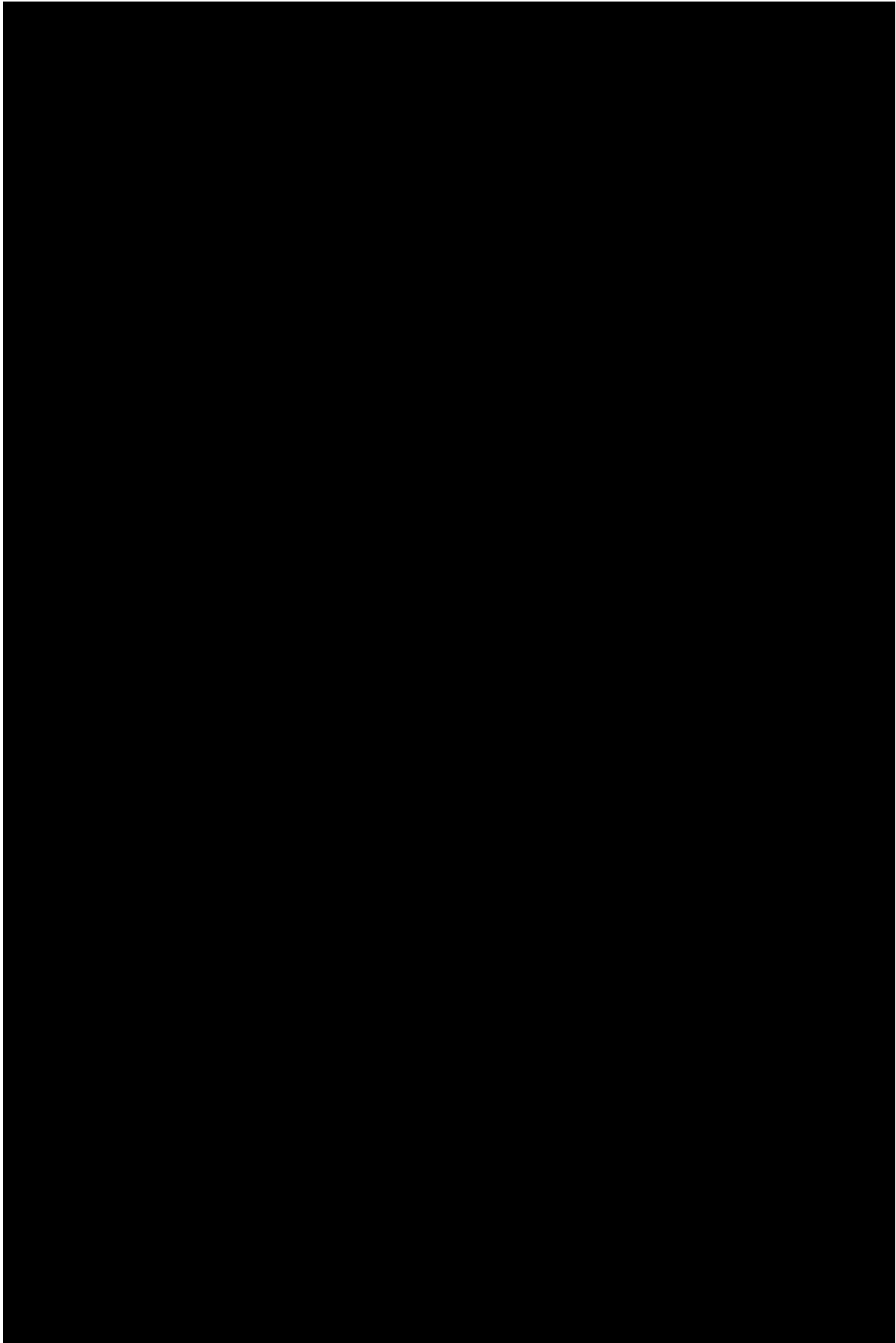
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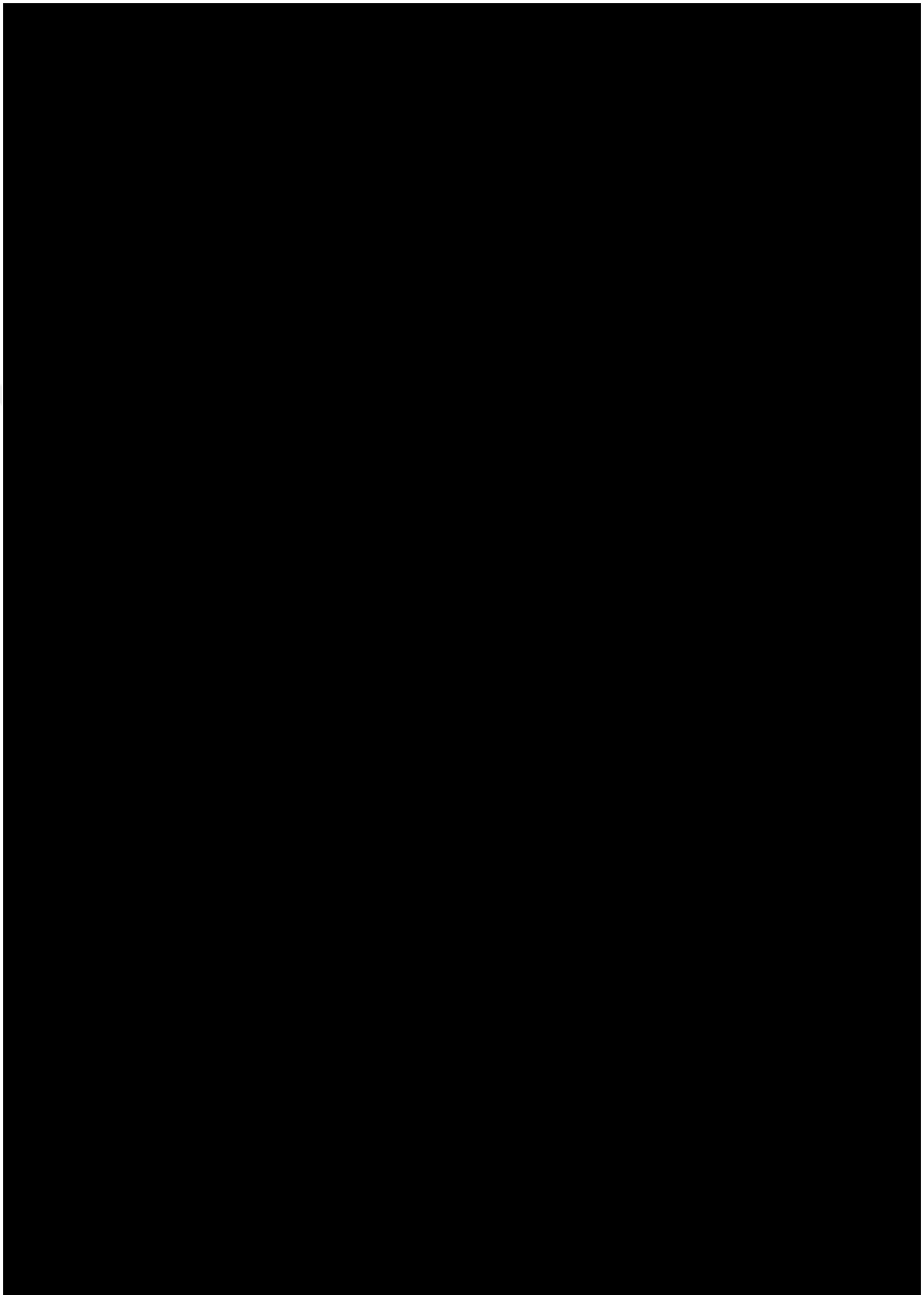
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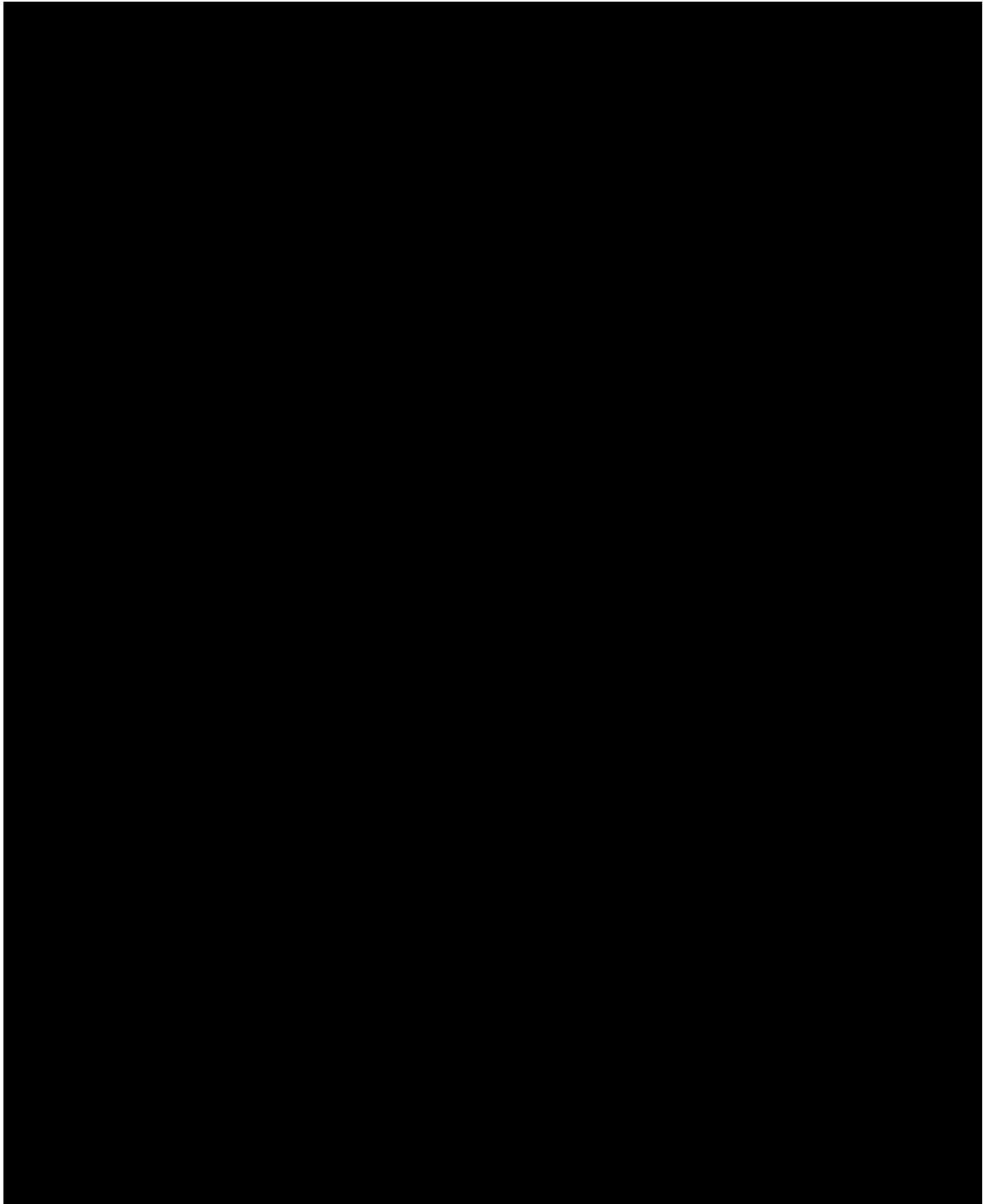
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APPENDICES

APPENDIX 1a. Effect of Factors on Morphological Parameters by Three-Way ANOVA Test. Symbols; n.s.: non-significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ represent significance levels of factors and their interactions on parameters.

	Height	Leaf	RWC (%)	Shoot FW	Root FW	Root DW	Leaf Area
Seed Priming (P)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
PGPB (B)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
Salt Stress (S)	***	***	***	***	***	***	***
P * B	n.s.	n.s.	n.s.	n.s.	***	**	n.s.
P * S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
B * S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	**
P * B * S	n.s.	*	n.s.	*	***	n.s.	***

APPENDIX 1b. Effect of Factors on Dark-Adapted Chlorophyll Fluorescence Parameters by Three-Way ANOVA Test. Symbols; n.s.: non-significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ represent significance levels of factors and their interactions on parameters.

	Fo	Fm	ABS/RC	ETo/RC	Phi(Po)	PI abs
Seed Priming (P)	*	*	**	n.s.	**	**
PGPB (B)	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Salt Stress (S)	n.s.	***	***	***	***	***
P * B	*	n.s.	n.s.	n.s.	n.s.	n.s.
P * S	n.s.	n.s.	*	n.s.	**	n.s.
B * S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P * B * S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

APPENDIX 1c. Effect of Factors on Gas Exchange and Light-Adapted Chlorophyll Fluorescence Parameters by Three-Way ANOVA Test. Symbols; n.s.: non-significant, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ represent significance levels of factors and their interactions on parameters.

	Gsw	ΦPSII	ETR	Fm'	H ₂ O _{leaf}	T _{leaf}
Seed Priming (P)	n.s.	n.s.	***	n.s.	***	***
PGPB (B)	n.s.	n.s.	*	n.s.	***	***
Salt Stress (S)	***	***	*	***	***	***
P * B	*	*	n.s.	**	***	***
P * S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
B * S	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
P * B * S	***	*	n.s.	n.s.	***	***

APPENDIX 2a. Results of Multiple Comparison LSD Test for Plant Stem Length

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	31.94	26.34 to 37.54	Yes	***	<.001	A-B
0 vs. B	8.375	2.773 to 13.98	Yes	**	0.004	A-C
0 vs. BS	33.06	27.46 to 38.66	Yes	***	<.001	A-D
0 vs. P	6.063	0.4602 to 11.66	Yes	*	0.034	A-E
0 vs. PS	32.31	26.71 to 37.91	Yes	***	<.001	A-F
0 vs. PB	5.188	-0.4148 to 10.79	No	ns	0.069	A-G
0 vs. PBS	33.69	28.09 to 39.29	Yes	***	<.001	A-H
S vs. B	-23.56	-29.16 to -17.96	Yes	***	<.001	B-C
S vs. BS	1.125	-4.477 to 6.727	No	ns	0.689	B-D
S vs. P	-25.88	-31.48 to -20.27	Yes	***	<.001	B-E
S vs. PS	0.375	-5.227 to 5.977	No	ns	0.894	B-F
S vs. PB	-26.75	-32.35 to -21.15	Yes	***	<.001	B-G
S vs. PBS	1.75	-3.852 to 7.352	No	ns	0.534	B-H
B vs. BS	24.69	19.09 to 30.29	Yes	***	<.001	C-D
B vs. P	-2.313	-7.915 to 3.290	No	ns	0.412	C-E
B vs. PS	23.94	18.34 to 29.54	Yes	***	<.001	C-F
B vs. PB	-3.188	-8.790 to 2.415	No	ns	0.259	C-G
B vs. PBS	25.31	19.71 to 30.91	Yes	***	<.001	C-H
BS vs. P	-27	-32.60 to -21.40	Yes	***	<.001	D-E
BS vs. PS	-0.75	-6.352 to 4.852	No	ns	0.79	D-F
BS vs. PB	-27.88	-33.48 to -22.27	Yes	***	<.001	D-G
BS vs. PBS	0.625	-4.977 to 6.227	No	ns	0.824	D-H
P vs. PS	26.25	20.65 to 31.85	Yes	***	<.001	E-F
P vs. PB	-0.875	-6.477 to 4.727	No	ns	0.756	E-G
P vs. PBS	27.63	22.02 to 33.23	Yes	***	<.001	E-H
PS vs. PB	-27.13	-32.73 to -21.52	Yes	***	<.001	F-G
PS vs. PBS	1.375	-4.227 to 6.977	No	ns	0.625	F-H
PB vs. PBS	28.5	22.90 to 34.10	Yes	***	<.001	G-H
Compact letter display						
0	A					
PB	A B					
P	B					
B	B					
S	C					
PS	C					

BS	C
PBS	C

APPENDIX 2b. Results of Multiple Comparison LSD Test for Plant Leaf Number

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	12.00	8.962 to 15.04	Yes	***	<.001	A-B
0 vs. B	1.375	-1.663 to 4.413	No	ns	.368	A-C
0 vs. BS	11.88	8.837 to 14.91	Yes	***	<.001	A-D
0 vs. P	2.875	-0.1628 to 5.913	No	ns	.063	A-E
0 vs. PS	8.875	5.837 to 11.91	Yes	***	<.001	A-F
0 vs. PB	1.000	-2.038 to 4.038	No	ns	.512	A-G
0 vs. PBS	12.38	9.337 to 15.41	Yes	***	<.001	A-H
S vs. B	-10.63	-13.66 to -7.587	Yes	***	<.001	B-C
S vs. BS	-0.1250	-3.163 to 2.913	No	ns	.935	B-D
S vs. P	-9.125	-12.16 to -6.087	Yes	***	<.001	B-E
S vs. PS	-3.125	-6.163 to - 0.08716	Yes	*	.044	B-F
S vs. PB	-11.00	-14.04 to -7.962	Yes	***	<.001	B-G
S vs. PBS	0.3750	-2.663 to 3.413	No	ns	.806	B-H
B vs. BS	10.50	7.462 to 13.54	Yes	***	<.001	C-D
B vs. P	1.500	-1.538 to 4.538	No	ns	.327	C-E
B vs. PS	7.500	4.462 to 10.54	Yes	***	<.001	C-F
B vs. PB	-0.3750	-3.413 to 2.663	No	ns	.806	C-G
B vs. PBS	11.00	7.962 to 14.04	Yes	***	<.001	C-H
BS vs. P	-9.000	-12.04 to -5.962	Yes	***	<.001	D-E
BS vs. PS	-3.000	-6.038 to 0.03784	No	ns	.053	D-F
BS vs. PB	-10.88	-13.91 to -7.837	Yes	***	<.001	D-G
BS vs. PBS	0.5000	-2.538 to 3.538	No	ns	.743	D-H
P vs. PS	6.000	2.962 to 9.038	Yes	***	<.001	E-F
P vs. PB	-1.875	-4.913 to 1.163	No	ns	.221	E-G
P vs. PBS	9.500	6.462 to 12.54	Yes	***	<.001	E-H
PS vs. PB	-7.875	-10.91 to -4.837	Yes	***	<.001	F-G
PS vs. PBS	3.500	0.4622 to 6.538	Yes	*	.025	F-H
PB vs. PBS	11.38	8.337 to 14.41	Yes	***	<.001	G-H

**Compact
letter display**

0	A
PB	A
B	A
P	A
PS	B

BS	B C
S	C
PBS	C

APPENDIX 2c. Results of Multiple Comparison LSD Test for Plant Fresh Shoot Weight

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	50.02	43.97 to 56.07	Yes	***	<.001	A-B
0 vs. B	2.771	-3.279 to 8.821	No	ns	.363	A-C
0 vs. BS	46.58	40.32 to 52.85	Yes	***	<.001	A-D
0 vs. P	6.724	0.6735 to 12.77	Yes	*	.030	A-E
0 vs. PS	44.43	38.38 to 50.48	Yes	***	<.001	A-F
0 vs. PB	5.955	-0.09562 to 12.00	No	ns	.054	A-G
0 vs. PBS	51.82	45.77 to 57.87	Yes	***	<.001	A-H
S vs. B	-47.25	-53.30 to -41.20	Yes	***	<.001	B-C
S vs. BS	-3.441	-9.704 to 2.821	No	ns	.276	B-D
S vs. P	-43.30	-49.35 to -37.25	Yes	***	<.001	B-E
S vs. PS	-5.591	-11.64 to 0.4597	No	ns	.069	B-F
S vs. PB	-44.07	-50.12 to -38.02	Yes	***	<.001	B-G
S vs. PBS	1.797	-4.253 to 7.847	No	ns	.554	B-H
B vs. BS	43.81	37.55 to 50.07	Yes	***	<.001	C-D
B vs. P	3.952	-2.098 to 10.00	No	ns	.196	C-E
B vs. PS	41.66	35.61 to 47.71	Yes	***	<.001	C-F
B vs. PB	3.183	-2.867 to 9.234	No	ns	.296	C-G
B vs. PBS	49.05	43.00 to 55.10	Yes	***	<.001	C-H
BS vs. P	-39.86	-46.12 to -33.60	Yes	***	<.001	D-E
BS vs. PS	-2.149	-8.412 to 4.113	No	ns	.494	D-F
BS vs. PB	-40.63	-46.89 to -34.37	Yes	***	<.001	D-G
BS vs. PBS	5.238	-1.024 to 11.50	No	ns	.099	D-H
P vs. PS	37.71	31.66 to 43.76	Yes	***	<.001	E-F
P vs. PB	-0.7691	-6.819 to 5.281	No	ns	.800	E-G
P vs. PBS	45.10	39.05 to 51.15	Yes	***	<.001	E-H
PS vs. PB	-38.48	-44.53 to -32.43	Yes	***	<.001	F-G
PS vs. PBS	7.388	1.337 to 13.44	Yes	*	.018	F-H
PB vs. PBS	45.87	39.82 to 51.92	Yes	***	<.001	G-H

Compact letter display

0	A
B	A B
PB	A B
P	B

PS	C
BS	C D
S	C D
PBS	D

APPENDIX 2d. Results of Multiple Comparison LSD Test for Plant Root Dry Weight

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	0.2471	0.1603 to 0.3339	Yes	***	<.001	A-B
0 vs. B	-0.1320	-0.2188 to - 0.04519	Yes	**	.004	A-C
0 vs. BS	0.2289	0.1421 to 0.3157	Yes	***	<.001	A-D
0 vs. P	-0.1211	-0.2079 to - 0.03431	Yes	**	.007	A-E
0 vs. PS	0.2524	0.1656 to 0.3392	Yes	***	<.001	A-F
0 vs. PB	-0.02637	-0.1132 to 0.06044	No	ns	.545	A-G
0 vs. PBS	0.2895	0.2027 to 0.3763	Yes	***	<.001	A-H
S vs. B	-0.3791	-0.4659 to - 0.2923	Yes	***	<.001	B-C
S vs. BS	-0.01825	-0.1051 to 0.06856	No	ns	.675	B-D
S vs. P	-0.3683	-0.4551 to - 0.2814	Yes	***	<.001	B-E
S vs. PS	0.005250	-0.08156 to 0.09206	No	ns	.904	B-F
S vs. PB	-0.2735	-0.3603 to - 0.1867	Yes	***	<.001	B-G
S vs. PBS	0.04238	-0.04444 to 0.1292	No	ns	.332	B-H
B vs. BS	0.3609	0.2741 to 0.4477	Yes	***	<.001	C-D
B vs. P	0.01088	-0.07594 to 0.09769	No	ns	.803	C-E
B vs. PS	0.3844	0.2976 to 0.4712	Yes	***	<.001	C-F
B vs. PB	0.1056	0.01881 to 0.1924	Yes	*	.018	C-G
B vs. PBS	0.4215	0.3347 to 0.5083	Yes	***	<.001	C-H
BS vs. P	-0.3500	-0.4368 to - 0.2632	Yes	***	<.001	D-E
BS vs. PS	0.02350	-0.06331 to 0.1103	No	ns	.590	D-F
BS vs. PB	-0.2553	-0.3421 to - 0.1684	Yes	***	<.001	D-G
BS vs. PBS	0.06063	-0.02619 to 0.1474	No	ns	.167	D-H
P vs. PS	0.3735	0.2867 to 0.4603	Yes	***	<.001	E-F
P vs. PB	0.09475	0.007940 to 0.1816	Yes	*	.033	E-G
P vs. PBS	0.4106	0.3238 to 0.4974	Yes	***	<.001	E-H

PS vs. PB	-0.2788	-0.3656 to -0.1919	Yes	***	<.001	F-G
PS vs. PBS	0.03713	-0.04969 to 0.1239	No	ns	.395	F-H
PB vs. PBS	0.3159	0.2291 to 0.4027	Yes	***	<.001	G-H
Compact letter display						
B	A					
P	A					
PB	B					
0	B					
BS	C					
S	C					
PS	C					
PBS	C					

APPENDIX 2e. Results of Multiple Comparison LSD Test for Plant Leaf Area

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	17.03	0.6523 to 33.40	Yes	*	.042	A-B
0 vs. B	-5.045	-21.42 to 11.33	No	ns	.540	A-C
0 vs. BS	9.369	-7.582 to 26.32	No	ns	.273	A-D
0 vs. P	10.70	-5.672 to 27.08	No	ns	.196	A-E
0 vs. PS	10.20	-6.176 to 26.58	No	ns	.217	A-F
0 vs. PB	-37.79	-54.17 to -21.42	Yes	***	<.001	A-G
0 vs. PBS	18.92	2.543 to 35.29	Yes	*	.024	A-H
S vs. B	-22.07	-38.45 to -5.698	Yes	**	.009	B-C
S vs. BS	-7.660	-24.61 to 9.291	No	ns	.369	B-D
S vs. P	-6.325	-22.70 to 10.05	No	ns	.442	B-E
S vs. PS	-6.829	-23.20 to 9.548	No	ns	.407	B-F
S vs. PB	-54.82	-71.20 to -38.45	Yes	***	<.001	B-G
S vs. PBS	1.890	-14.49 to 18.27	No	ns	.818	B-H
B vs. BS	14.41	-2.537 to 31.37	No	ns	.094	C-D
B vs. P	15.75	-0.6269 to 32.13	No	ns	.059	C-E
B vs. PS	15.25	-1.131 to 31.62	No	ns	.067	C-F
B vs. PB	-32.75	-49.13 to -16.37	Yes	***	<.001	C-G
B vs. PBS	23.96	7.588 to 40.34	Yes	**	.005	C-H
BS vs. P	1.335	-15.62 to 18.29	No	ns	.875	D-E
BS vs. PS	0.8310	-16.12 to 17.78	No	ns	.922	D-F
BS vs. PB	-47.16	-64.11 to -30.21	Yes	***	<.001	D-G
BS vs. PBS	9.550	-7.401 to 26.50	No	ns	.264	D-H
P vs. PS	-0.5041	-16.88 to 15.87	No	ns	.951	E-F

P vs. PB	-48.50	-64.87 to -32.12	Yes	***	<.001	E-G
P vs. PBS	8.215	-8.161 to 24.59	No	ns	.319	E-H
PS vs. PB	-47.99	-64.37 to -31.62	Yes	***	<.001	F-G
PS vs. PBS	8.719	-7.657 to 25.10	No	ns	.291	F-H
PB vs. PBS	56.71	40.34 to 73.09	Yes	***	<.001	G-H

**Compact
letter display**

PB	A
B	B
0	B
BS	B C
PS	B C
P	B C
S	C
PBS	C

APPENDIX 3. Results of Multiple Comparison LSD Test for Relative Membrane Permeability

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	-63.16	-75.73 to -50.59	Yes	***	<.001	A-B
0 vs. B	-6.678	-18.82 to 5.466	No	ns	.275	A-C
0 vs. BS	-56.01	-69.13 to -42.90	Yes	***	<.001	A-D
0 vs. P	6.464	-5.680 to 18.61	No	ns	.290	A-E
0 vs. PS	-72.88	-85.03 to -60.74	Yes	***	<.001	A-F
0 vs. PB	9.686	-2.457 to 21.83	No	ns	.116	A-G
0 vs. PBS	-60.74	-73.31 to -48.17	Yes	***	<.001	A-H
S vs. B	56.48	43.91 to 69.05	Yes	***	<.001	B-C
S vs. BS	7.142	-6.370 to 20.65	No	ns	.294	B-D
S vs. P	69.62	57.05 to 82.19	Yes	***	<.001	B-E
S vs. PS	-9.728	-22.30 to 2.842	No	ns	.126	B-F
S vs. PB	72.84	60.27 to 85.41	Yes	***	<.001	B-G
S vs. PBS	2.413	-10.57 to 15.39	No	ns	.711	B-H
B vs. BS	-49.34	-62.45 to -36.22	Yes	***	<.001	C-D
B vs. P	13.14	0.9978 to 25.28	Yes	*	.034	C-E
B vs. PS	-66.21	-78.35 to -54.06	Yes	***	<.001	C-F
B vs. PB	16.36	4.220 to 28.51	Yes	**	.009	C-G
B vs. PBS	-54.07	-66.64 to -41.50	Yes	***	<.001	C-H
BS vs. P	62.48	49.36 to 75.59	Yes	***	<.001	D-E
BS vs. PS	-16.87	-29.99 to -3.754	Yes	*	.013	D-F
BS vs. PB	65.70	52.58 to 78.82	Yes	***	<.001	D-G
BS vs. PBS	-4.730	-18.24 to 8.782	No	ns	.486	D-H
P vs. PS	-79.35	-91.49 to -67.20	Yes	***	<.001	E-F
P vs. PB	3.223	-8.921 to 15.37	No	ns	.597	E-G
P vs. PBS	-67.21	-79.78 to -54.64	Yes	***	<.001	E-H
PS vs. PB	82.57	70.43 to 94.71	Yes	***	<.001	F-G
PS vs. PBS	12.14	-0.4288 to 24.71	No	ns	.058	F-H
PB vs. PBS	-70.43	-83.00 to -57.86	Yes	***	<.001	G-H
Compact letter display						
PS	A					
S	A B					

PBS	A B
BS	B
B	C
0	C D
P	D
PB	D



APPENDIX 4. Results of Multiple Comparison LSD Test for Relative Water Content

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	12.79	4.659 to 20.92	Yes	**	.003	A-B
0 vs. B	-0.7689	-8.898 to 7.361	No	ns	.850	A-C
0 vs. BS	11.89	3.477 to 20.31	Yes	**	.006	A-D
0 vs. P	-0.7449	-8.874 to 7.385	No	ns	.855	A-E
0 vs. PS	11.85	3.721 to 19.98	Yes	**	.005	A-F
0 vs. PB	2.498	-5.631 to 10.63	No	ns	.541	A-G
0 vs. PBS	10.45	2.320 to 18.58	Yes	*	.013	A-H
S vs. B	-13.56	-21.69 to -5.428	Yes	**	.002	B-C
S vs. BS	-0.8967	-9.311 to 7.518	No	ns	.832	B-D
S vs. P	-13.53	-21.66 to -5.404	Yes	**	.002	B-E
S vs. PS	-0.9381	-9.068 to 7.191	No	ns	.818	B-F
S vs. PB	-10.29	-18.42 to -2.161	Yes	*	.014	B-G
S vs. PBS	-2.340	-10.47 to 5.790	No	ns	.566	B-H
B vs. BS	12.66	4.246 to 21.08	Yes	**	.004	C-D
B vs. P	0.02399	-8.105 to 8.153	No	ns	.995	C-E
B vs. PS	12.62	4.490 to 20.75	Yes	**	.003	C-F
B vs. PB	3.267	-4.862 to 11.40	No	ns	.424	C-G
B vs. PBS	11.22	3.088 to 19.35	Yes	**	.008	C-H
BS vs. P	-12.64	-21.05 to -4.222	Yes	**	.004	D-E
BS vs. PS	-0.04138	-8.456 to 8.373	No	ns	.992	D-F
BS vs. PB	-9.394	-17.81 to -0.9788	Yes	*	.029	D-G
BS vs. PBS	-1.443	-9.858 to 6.972	No	ns	.732	D-H
P vs. PS	12.60	4.466 to 20.72	Yes	**	.003	E-F
P vs. PB	3.243	-4.886 to 11.37	No	ns	.427	E-G
P vs. PBS	11.19	3.064 to 19.32	Yes	**	.008	E-H
PS vs. PB	-9.352	-17.48 to -1.223	Yes	*	.025	F-G
PS vs. PBS	-1.401	-9.531 to 6.728	No	ns	.731	F-H
PB vs. PBS	7.951	-0.1787 to 16.08	No	ns	.055	G-H
Compact letter display						
B	A					
P	A					
0	A					
PB	A B					
PBS	B C					
PS	C					
BS	C					
S	C					

APPENDIX 5a. Results of Multiple Comparison LSD Test for Fo (Minimum Fluorescence)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	439.0	58.80 to 819.3	Yes	*	.024	A-B
0 vs. B	126.1	-254.1 to 506.4	No	ns	.509	A-C
0 vs. BS	347.7	-45.86 to 741.3	No	ns	.082	A-D
0 vs. P	113.4	-266.9 to 493.6	No	ns	.553	A-E
0 vs. PS	336.3	-43.94 to 716.5	No	ns	.082	A-F
0 vs. PB	-43.38	-423.6 to 336.9	No	ns	.820	A-G
0 vs. PBS	-251.1	-631.4 to 129.1	No	ns	.191	A-H
S vs. B	-312.9	-693.2 to 67.33	No	ns	.105	B-C
S vs. BS	-91.31	-484.9 to 302.3	No	ns	.644	B-D
S vs. P	-325.7	-705.9 to 54.58	No	ns	.092	B-E
S vs. PS	-102.7	-483.0 to 277.5	No	ns	.590	B-F
S vs. PB	-482.4	-862.7 to -102.2	Yes	*	.014	B-G
S vs. PBS	-690.2	-1070 to -309.9	Yes	***	<.001	B-H
B vs. BS	221.6	-172.0 to 615.2	No	ns	.264	C-D
B vs. P	-12.75	-393.0 to 367.5	No	ns	.947	C-E
B vs. PS	210.2	-170.1 to 590.4	No	ns	.273	C-F
B vs. PB	-169.5	-549.7 to 210.7	No	ns	.376	C-G
B vs. PBS	-377.3	-757.5 to 2.994	No	ns	.052	C-H
BS vs. P	-234.4	-627.9 to 159.2	No	ns	.238	D-E
BS vs. PS	-11.43	-405.0 to 382.2	No	ns	.954	D-F
BS vs. PB	-391.1	-784.7 to 2.483	No	ns	.051	D-G
BS vs. PBS	-598.9	-992.4 to -205.3	Yes	**	.004	D-H
P vs. PS	222.9	-157.3 to 603.2	No	ns	.245	E-F
P vs. PB	-156.8	-537.0 to 223.5	No	ns	.412	E-G
P vs. PBS	-364.5	-744.7 to 15.74	No	ns	.060	E-H
PS vs. PB	-379.7	-759.9 to 0.5653	No	ns	.050	F-G
PS vs. PBS	-587.4	-967.7 to -207.2	Yes	**	.003	F-H
PB vs. PBS	-207.8	-588.0 to 172.5	No	ns	.278	G-H
Compact letter display						
PBS	A					
PB	A B					
0	A B					
P	A C					
B	A C					
PS	B C					

BS	B C
S	C

APPENDIX 5b. Results of Multiple Comparison LSD Test for Fm (Maximum Fluorescence)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	7982	5410 to 10553	Yes	***	<.001	A-B
0 vs. B	39.46	-2532 to 2611	No	ns	.976	A-C
0 vs. BS	7418	4769 to 10067	Yes	***	<.001	A-D
0 vs. P	382.0	-2189 to 2953	No	ns	.767	A-E
0 vs. PS	10420	7848 to 12991	Yes	***	<.001	A-F
0 vs. PB	-448.3	-3020 to 2123	No	ns	.728	A-G
0 vs. PBS	10445	7873 to 13016	Yes	***	<.001	A-H
S vs. B	-7942	-10323 to -5562	Yes	***	<.001	B-C
S vs. BS	-563.7	-3028 to 1900	No	ns	.648	B-D
S vs. P	-7600	-9981 to -5219	Yes	***	<.001	B-E
S vs. PS	2438	57.08 to 4818	Yes	*	.045	B-F
S vs. PB	-8430	-10811 to -6049	Yes	***	<.001	B-G
S vs. PBS	2463	82.22 to 4843	Yes	*	.043	B-H
B vs. BS	7379	4914 to 9843	Yes	***	<.001	C-D
B vs. P	342.5	-2038 to 2723	No	ns	.774	C-E
B vs. PS	10380	7999 to 12761	Yes	***	<.001	C-F
B vs. PB	-487.8	-2868 to 1893	No	ns	.683	C-G
B vs. PBS	10405	8025 to 12786	Yes	***	<.001	C-H
BS vs. P	-7036	-9500 to -4572	Yes	***	<.001	D-E
BS vs. PS	3001	537.2 to 5466	Yes	*	.018	D-F
BS vs. PB	-7866	-10331 to -5402	Yes	***	<.001	D-G
BS vs. PBS	3027	562.4 to 5491	Yes	*	.017	D-H
P vs. PS	10038	7657 to 12418	Yes	***	<.001	E-F
P vs. PB	-830.3	-3211 to 1550	No	ns	.487	E-G
P vs. PBS	10063	7682 to 12443	Yes	***	<.001	E-H
PS vs. PB	-10868	-13248 to -8487	Yes	***	<.001	F-G
PS vs. PBS	25.14	-2355 to 2406	No	ns	.983	F-H
PB vs. PBS	10893	8512 to 13274	Yes	***	<.001	G-H
Compact letter display						
PB	A					
0	A					
B	A					

P	A
BS	B
S	B
PS	C
PBS	C

APPENDIX 5c. Results of Multiple Comparison LSD Test for ABS/RC (Effective Absorption Flux per Reaction Center)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	-0.9414	-1.270 to -0.6123	Yes	***	<.001	A-B
0 vs. B	0.01854	-0.3105 to 0.3476	No	ns	.910	A-C
0 vs. BS	-0.8419	-1.183 to -0.5013	Yes	***	<.001	A-D
0 vs. P	-0.02623	-0.3553 to 0.3029	No	ns	.874	A-E
0 vs. PS	-1.231	-1.560 to -0.9015	Yes	***	<.001	A-F
0 vs. PB	0.01494	-0.3141 to 0.3440	No	ns	.928	A-G
0 vs. PBS	-1.509	-1.850 to -1.169	Yes	***	<.001	A-H
S vs. B	0.9599	0.6309 to 1.289	Yes	***	<.001	B-C
S vs. BS	0.09947	-0.2412 to 0.4401	No	ns	.561	B-D
S vs. P	0.9152	0.5861 to 1.244	Yes	***	<.001	B-E
S vs. PS	-0.2892	-0.6183 to 0.03990	No	ns	.084	B-F
S vs. PB	0.9563	0.6273 to 1.285	Yes	***	<.001	B-G
S vs. PBS	-0.5678	-0.9084 to - 0.2272	Yes	**	.002	B-H
B vs. BS	-0.8605	-1.201 to -0.5199	Yes	***	<.001	C-D
B vs. P	-0.04476	-0.3738 to 0.2843	No	ns	.786	C-E
B vs. PS	-1.249	-1.578 to -0.9200	Yes	***	<.001	C-F
B vs. PB	- 0.003600	-0.3327 to 0.3255	No	ns	.983	C-G
B vs. PBS	-1.528	-1.868 to -1.187	Yes	***	<.001	C-H
BS vs. P	0.8157	0.4751 to 1.156	Yes	***	<.001	D-E
BS vs. PS	-0.3886	-0.7293 to - 0.04802	Yes	*	.026	D-F
BS vs. PB	0.8569	0.5163 to 1.198	Yes	***	<.001	D-G
BS vs. PBS	-0.6673	-1.019 to -0.3155	Yes	***	<.001	D-H
P vs. PS	-1.204	-1.533 to -0.8753	Yes	***	<.001	E-F
P vs. PB	0.04116	-0.2879 to 0.3702	No	ns	.803	E-G
P vs. PBS	-1.483	-1.824 to -1.142	Yes	***	<.001	E-H
PS vs. PB	1.246	0.9164 to 1.575	Yes	***	<.001	F-G

PS vs. PBS	-0.2786	-0.6192 to 0.06200	No	ns	.107	F-H
PB vs. PBS	-1.524	-1.865 to -1.184	Yes	***	<.001	G-H
Compact letter display						
PBS	A					
PS	A B					
S	B C					
BS	C					
P	D					
0	D					
PB	D					
B	D					

APPENDIX 5d. Results of Multiple Comparison LSD Test for ETo/RC (Electron Transport Rate Beyond Plastoquinone-A)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	-0.1456	-0.2000 to -0.09133	Yes	***	<.001	A-B
0 vs. B	0.01690	-0.03741 to 0.07121	No	ns	.535	A-C
0 vs. BS	-0.07726	-0.1335 to -0.02105	Yes	**	.008	A-D
0 vs. P	0.02935	-0.02496 to 0.08366	No	ns	.283	A-E
0 vs. PS	-0.03729	-0.09160 to 0.01702	No	ns	.174	A-F
0 vs. PB	0.007513	-0.04680 to 0.06182	No	ns	.783	A-G
0 vs. PBS	-0.1350	-0.1912 to -0.07878	Yes	***	<.001	A-H
S vs. B	0.1625	0.1082 to 0.2169	Yes	***	<.001	B-C
S vs. BS	0.06838	0.01217 to 0.1246	Yes	*	.018	B-D
S vs. P	0.1750	0.1207 to 0.2293	Yes	***	<.001	B-E
S vs. PS	0.1084	0.05404 to 0.1627	Yes	***	<.001	B-F
S vs. PB	0.1532	0.09885 to 0.2075	Yes	***	<.001	B-G
S vs. PBS	0.01065	-0.04557 to 0.06686	No	ns	.706	B-H
B vs. BS	-0.09416	-0.1504 to -0.03795	Yes	**	.001	C-D
B vs. P	0.01245	-0.04186 to 0.06676	No	ns	.648	C-E
B vs. PS	-0.05419	-0.1085 to 0.0001191	No	ns	.050	C-F
B vs. PB	-0.009387	-0.06370 to 0.04492	No	ns	.730	C-G

B vs. PBS	-0.1519	-0.2081 to -0.09568	Yes	***	<.001	C-H
BS vs. P	0.1066	0.05040 to 0.1628	Yes	***	<.001	D-E
BS vs. PS	0.03997	-0.01624 to 0.09619	No	ns	.160	D-F
BS vs. PB	0.08477	0.02856 to 0.1410	Yes	**	.004	D-G
BS vs. PBS	-0.05773	-0.1158 to 0.0003234	No	ns	.051	D-H
P vs. PS	-0.06664	-0.1209 to -0.01233	Yes	*	.017	E-F
P vs. PB	-0.02184	-0.07615 to 0.03247	No	ns	.424	E-G
P vs. PBS	-0.1643	-0.2206 to -0.1081	Yes	***	<.001	E-H
PS vs. PB	0.04480	-0.009507 to 0.09911	No	ns	.104	F-G
PS vs. PBS	-0.09771	-0.1539 to -0.04149	Yes	***	<.001	F-H
PB vs. PBS	-0.1425	-0.1987 to -0.08629	Yes	***	<.001	G-H
Compact letter display						
S	A					
PBS	A B					
BS	B C					
PS	C D					
0	D E					
PB	D E					
B	D E					
P	E					

APPENDIX 5e. Results of Multiple Comparison LSD Test for PI_{ABS} (Performance Index on an Absorption Basis)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	5.359	4.232 to 6.485	Yes	***	<.001	A-B
0 vs. B	0.1718	-0.9550 to 1.299	No	ns	.761	A-C
0 vs. BS	5.194	4.028 to 6.360	Yes	***	<.001	A-D
0 vs. P	1.205	0.07837 to 2.332	Yes	*	.037	A-E
0 vs. PS	6.601	5.434 to 7.767	Yes	***	<.001	A-F
0 vs. PB	0.04250	-1.084 to 1.169	No	ns	.940	A-G
0 vs. PBS	6.684	5.557 to 7.810	Yes	***	<.001	A-H
S vs. B	-5.187	-6.314 to -4.060	Yes	***	<.001	B-C
S vs. BS	-0.1646	-1.331 to 1.002	No	ns	.778	B-D
S vs. P	-4.153	-5.280 to -3.027	Yes	***	<.001	B-E
S vs. PS	1.242	0.07572 to 2.408	Yes	*	.037	B-F

S vs. PB	-5.316	-6.443 to -4.189	Yes	***	<.001	B-G
S vs. PBS	1.325	0.1984 to 2.452	Yes	*	.022	B-H
B vs. BS	5.022	3.856 to 6.188	Yes	***	<.001	C-D
B vs. P	1.033	-0.09338 to 2.160	No	ns	.071	C-E
B vs. PS	6.429	5.263 to 7.595	Yes	***	<.001	C-F
B vs. PB	-0.1293	-1.256 to 0.9975	No	ns	.819	C-G
B vs. PBS	6.512	5.385 to 7.639	Yes	***	<.001	C-H
BS vs. P	-3.989	-5.155 to -2.823	Yes	***	<.001	D-E
BS vs. PS	1.407	0.2021 to 2.611	Yes	*	.023	D-F
BS vs. PB	-5.151	-6.318 to -3.985	Yes	***	<.001	D-G
BS vs. PBS	1.490	0.3234 to 2.656	Yes	*	.013	D-H
P vs. PS	5.395	4.229 to 6.562	Yes	***	<.001	E-F
P vs. PB	-1.163	-2.289 to -0.03587	Yes	*	.043	E-G
P vs. PBS	5.479	4.352 to 6.605	Yes	***	<.001	E-H
PS vs. PB	-6.558	-7.724 to -5.392	Yes	***	<.001	F-G
PS vs. PBS	0.08310	-1.083 to 1.249	No	ns	.887	F-H
PB vs. PBS	6.641	5.514 to 7.768	Yes	***	<.001	G-H
Compact letter display						
0	A					
PB	A					
B	A B					
P	B					
BS	C					
S	C					
PS	D					
PBS	D					

APPENDIX 5f. Results of Multiple Comparison LSD Test for ΦPo (Fv/Fm, Maximum Quantum Yield of PSII Primary Photochemistry)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	0.05955	0.01554 to 0.1035	Yes	**	.009	A-B
0 vs. B	0.001850	-0.04215 to 0.04585	No	ns	.933	A-C
0 vs. BS	0.05887	0.01332 to 0.1044	Yes	*	.012	A-D
0 vs. P	0.004487	-0.03951 to 0.04849	No	ns	.839	A-E
0 vs. PS	0.1026	0.05861 to 0.1466	Yes	***	<.001	A-F
0 vs. PB	0.005487	-0.03851 to 0.04949	No	ns	.804	A-G
0 vs. PBS	0.1558	0.1118 to 0.1998	Yes	***	<.001	A-H
S vs. B	-0.05770	-0.1017 to -0.01369	Yes	*	.011	B-C

S vs. BS	-0.0006761	-0.04622 to 0.04487	No	ns	.976	B-D
S vs. P	-0.05506	-0.09906 to -0.01106	Yes	*	.015	B-E
S vs. PS	0.04307	-0.0009355 to 0.08707	No	ns	.055	B-F
S vs. PB	-0.05406	-0.09806 to -0.01006	Yes	*	.017	B-G
S vs. PBS	0.09630	0.05229 to 0.1403	Yes	***	<.001	B-H
B vs. BS	0.05702	0.01147 to 0.1026	Yes	*	.015	C-D
B vs. P	0.002637	-0.04136 to 0.04664	No	ns	.905	C-E
B vs. PS	0.1008	0.05676 to 0.1448	Yes	***	<.001	C-F
B vs. PB	0.003637	-0.04036 to 0.04764	No	ns	.869	C-G
B vs. PBS	0.1540	0.1100 to 0.1980	Yes	***	<.001	C-H
BS vs. P	-0.05438	-0.09993 to -0.008836	Yes	*	.020	D-E
BS vs. PS	0.04374	-0.001804 to 0.08929	No	ns	.059	D-F
BS vs. PB	-0.05338	-0.09893 to -0.007836	Yes	*	.022	D-G
BS vs. PBS	0.09697	0.05142 to 0.1425	Yes	***	<.001	D-H
P vs. PS	0.09813	0.05412 to 0.1421	Yes	***	<.001	E-F
P vs. PB	0.001000	-0.04300 to 0.04500	No	ns	.964	E-G
P vs. PBS	0.1514	0.1074 to 0.1954	Yes	***	<.001	E-H
PS vs. PB	-0.09713	-0.1411 to -0.05312	Yes	***	<.001	F-G
PS vs. PBS	0.05323	0.009226 to 0.09723	Yes	*	.019	F-H
PB vs. PBS	0.1504	0.1064 to 0.1944	Yes	***	<.001	G-H

**Compact
letter
display**

0	A
B	A
P	A
PB	A
BS	B
S	B
PS	B
PBS	C

APPENDIX 6a. Results of Multiple Comparison LSD Test for Gsw (Stomatal Conductance to Water Vapour)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	94.25	70.22 to 118.3	Yes	***	<.001	A-B
0 vs. B	63.05	39.84 to 86.27	Yes	***	<.001	A-C
0 vs. BS	91.94	67.91 to 116.0	Yes	***	<.001	A-D
0 vs. P	69.36	46.14 to 92.57	Yes	***	<.001	A-E
0 vs. PS	83.63	60.41 to 106.8	Yes	***	<.001	A-F
0 vs. PB	45.86	22.64 to 69.07	Yes	***	<.001	A-G
0 vs. PBS	83.04	59.83 to 106.3	Yes	***	<.001	A-H
S vs. B	-31.20	-55.23 to -7.170	Yes	*	.012	B-C
S vs. BS	-2.312	-27.13 to 22.51	No	ns	.853	B-D
S vs. P	-24.89	-48.92 to -0.8640	Yes	*	.043	B-E
S vs. PS	-10.62	-34.65 to 13.41	No	ns	.379	B-F
S vs. PB	-48.39	-72.42 to -24.37	Yes	***	<.001	B-G
S vs. PBS	-11.21	-35.24 to 12.82	No	ns	.354	B-H
B vs. BS	28.89	4.858 to 52.92	Yes	*	.019	C-D
B vs. P	6.306	-16.91 to 29.52	No	ns	.588	C-E
B vs. PS	20.58	-2.638 to 43.79	No	ns	.081	C-F
B vs. PB	-17.20	-40.41 to 6.019	No	ns	.143	C-G
B vs. PBS	19.99	-3.224 to 43.20	No	ns	.090	C-H
BS vs. P	-22.58	-46.61 to 1.448	No	ns	.065	D-E
BS vs. PS	-8.311	-32.34 to 15.72	No	ns	.491	D-F
BS vs. PB	-46.08	-70.11 to -22.05	Yes	***	<.001	D-G
BS vs. PBS	-8.897	-32.93 to 15.13	No	ns	.461	D-H
P vs. PS	14.27	-8.944 to 37.49	No	ns	.223	E-F
P vs. PB	-23.50	-46.72 to -0.2867	Yes	*	.047	E-G
P vs. PBS	13.68	-9.530 to 36.90	No	ns	.242	E-H
PS vs. PB	-37.77	-60.99 to -14.56	Yes	**	.002	F-G
PS vs. PBS	-0.5859	-23.80 to 22.63	No	ns	.960	F-H
PB vs. PBS	37.19	13.97 to 60.40	Yes	**	.002	G-H
Compact letter display						
0	A					
PB	B					
B	B C					
P	C D					
PBS	C E					
PS	C E					
BS	D E					

APPENDIX 6b. Results of Multiple Comparison LSD Test for Φ PSII (Quantum Efficiency in Light)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	0.2989	0.2219 to 0.3758	Yes	***	<.001	A-B
0 vs. B	-0.003250	-0.08020 to 0.07370	No	ns	.933	A-C
0 vs. BS	0.1830	0.1034 to 0.2627	Yes	***	<.001	A-D
0 vs. P	0.009375	-0.06758 to 0.08633	No	ns	.808	A-E
0 vs. PS	0.2621	0.1852 to 0.3391	Yes	***	<.001	A-F
0 vs. PB	0.02150	-0.05545 to 0.09845	No	ns	.578	A-G
0 vs. PBS	0.3280	0.2510 to 0.4050	Yes	***	<.001	A-H
S vs. B	-0.3021	-0.3791 to -0.2252	Yes	***	<.001	B-C
S vs. BS	-0.1159	-0.1955 to -0.03621	Yes	**	.005	B-D
S vs. P	-0.2895	-0.3665 to -0.2125	Yes	***	<.001	B-E
S vs. PS	-0.03675	-0.1137 to 0.04020	No	ns	.343	B-F
S vs. PB	-0.2774	-0.3543 to -0.2004	Yes	***	<.001	B-G
S vs. PBS	0.02913	-0.04783 to 0.1061	No	ns	.451	B-H
B vs. BS	0.1863	0.1066 to 0.2659	Yes	***	<.001	C-D
B vs. P	0.01263	-0.06433 to 0.08958	No	ns	.744	C-E
B vs. PS	0.2654	0.1884 to 0.3423	Yes	***	<.001	C-F
B vs. PB	0.02475	-0.05220 to 0.1017	No	ns	.522	C-G
B vs. PBS	0.3313	0.2543 to 0.4082	Yes	***	<.001	C-H
BS vs. P	-0.1736	-0.2533 to -0.09399	Yes	***	<.001	D-E
BS vs. PS	0.07911	-0.0005445 to 0.1588	No	ns	.052	D-F
BS vs. PB	-0.1615	-0.2412 to -0.08187	Yes	***	<.001	D-G
BS vs. PBS	0.1450	0.06533 to 0.2246	Yes	***	<.001	D-H
P vs. PS	0.2528	0.1758 to 0.3297	Yes	***	<.001	E-F
P vs. PB	0.01212	-0.06483 to 0.08908	No	ns	.753	E-G
P vs. PBS	0.3186	0.2417 to 0.3956	Yes	***	<.001	E-H
PS vs. PB	-0.2406	-0.3176 to -0.1637	Yes	***	<.001	F-G
PS vs. PBS	0.06588	-0.01108 to 0.1428	No	ns	.092	F-H
PB vs. PBS	0.3065	0.2295 to 0.3835	Yes	***	<.001	G-H
Compact letter display						
B	A					

0	A
P	A
PB	A
BS	B
PS	B C
S	C
PBS	C

APPENDIX 6c. Results of Multiple Comparison LSD Test for Fm' (Maximum Fluorescence in Light-Adapted State)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	230.6	186.4 to 274.7	Yes	***	<.001	A-B
0 vs. B	-0.4134	-44.55 to 43.72	No	ns	.985	A-C
0 vs. BS	194.1	149.9 to 238.2	Yes	***	<.001	A-D
0 vs. P	1.661	-42.47 to 45.79	No	ns	.940	A-E
0 vs. PS	199.8	155.7 to 244.0	Yes	***	<.001	A-F
0 vs. PB	10.44	-33.70 to 54.57	No	ns	.637	A-G
0 vs. PBS	221.9	177.8 to 266.0	Yes	***	<.001	A-H
S vs. B	-231.0	-275.1 to -186.9	Yes	***	<.001	B-C
S vs. BS	-36.51	-80.65 to 7.620	No	ns	.103	B-D
S vs. P	-228.9	-273.1 to -184.8	Yes	***	<.001	B-E
S vs. PS	-30.74	-74.87 to 13.39	No	ns	.168	B-F
S vs. PB	-220.1	-264.3 to -176.0	Yes	***	<.001	B-G
S vs. PBS	-8.675	-52.81 to 35.46	No	ns	.695	B-H
B vs. BS	194.5	150.3 to 238.6	Yes	***	<.001	C-D
B vs. P	2.075	-42.06 to 46.21	No	ns	.925	C-E
B vs. PS	200.3	156.1 to 244.4	Yes	***	<.001	C-F
B vs. PB	10.85	-33.28 to 54.98	No	ns	.624	C-G
B vs. PBS	222.3	178.2 to 266.5	Yes	***	<.001	C-H
BS vs. P	-192.4	-236.5 to -148.3	Yes	***	<.001	D-E
BS vs. PS	5.774	-38.36 to 49.91	No	ns	.794	D-F
BS vs. PB	-183.6	-227.8 to -139.5	Yes	***	<.001	D-G
BS vs. PBS	27.84	-16.29 to 71.97	No	ns	.212	D-H
P vs. PS	198.2	154.0 to 242.3	Yes	***	<.001	E-F
P vs. PB	8.777	-35.36 to 52.91	No	ns	.692	E-G
P vs. PBS	220.2	176.1 to 264.4	Yes	***	<.001	E-H
PS vs. PB	-189.4	-233.5 to -145.3	Yes	***	<.001	F-G
PS vs. PBS	22.07	-22.07 to 66.20	No	ns	.321	F-H
PB vs. PBS	211.5	167.3 to 255.6	Yes	***	<.001	G-H

Compact
letter display

B	A
0	A
P	A
PB	A
BS	B
PS	B
PBS	B
S	B

APPENDIX 6d. Results of Multiple Comparison LSD Test for ETR (Electron Transport Rate)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	4.304	-14.26 to 22.87	No	ns	.644	A-B
0 vs. B	-5.364	-23.93 to 13.20	No	ns	.565	A-C
0 vs. BS	-7.991	-27.20 to 11.22	No	ns	.408	A-D
0 vs. P	-34.84	-53.40 to -16.28	Yes	***	<.001	A-E
0 vs. PS	-17.80	-36.36 to 0.7648	No	ns	.060	A-F
0 vs. PB	-49.08	-67.65 to -30.52	Yes	***	<.001	A-G
0 vs. PBS	-30.61	-49.17 to -12.05	Yes	**	.002	A-H
S vs. B	-9.667	-28.23 to 8.894	No	ns	.301	B-C
S vs. BS	-12.29	-31.51 to 6.919	No	ns	.205	B-D
S vs. P	-39.14	-57.70 to -20.58	Yes	***	<.001	B-E
S vs. PS	-22.10	-40.66 to -3.539	Yes	*	.020	B-F
S vs. PB	-53.39	-71.95 to -34.83	Yes	***	<.001	B-G
S vs. PBS	-34.91	-53.47 to -16.35	Yes	***	<.001	B-H
B vs. BS	-2.627	-21.84 to 16.59	No	ns	.785	C-D
B vs. P	-29.48	-48.04 to -10.91	Yes	**	.002	C-E
B vs. PS	-12.43	-30.99 to 6.128	No	ns	.185	C-F
B vs. PB	-43.72	-62.28 to -25.16	Yes	***	<.001	C-G
B vs. PBS	-25.25	-43.81 to -6.684	Yes	**	.009	C-H
BS vs. P	-26.85	-46.06 to -7.636	Yes	**	.007	D-E
BS vs. PS	-9.806	-29.02 to 9.407	No	ns	.311	D-F
BS vs. PB	-41.09	-60.31 to -21.88	Yes	***	<.001	D-G
BS vs. PBS	-22.62	-41.83 to -3.406	Yes	*	.022	D-H
P vs. PS	17.04	-1.519 to 35.60	No	ns	.071	E-F
P vs. PB	-14.24	-32.81 to 4.317	No	ns	.130	E-G
P vs. PBS	4.230	-14.33 to 22.79	No	ns	.650	E-H
PS vs. PB	-31.29	-49.85 to -12.73	Yes	**	.001	F-G
PS vs. PBS	-12.81	-31.37 to 5.749	No	ns	.172	F-H
PB vs. PBS	18.48	-0.08643 to 37.04	No	ns	.051	G-H

**Compact
letter display**

PB	A
P	A B
PBS	A B
PS	B C
BS	C D
B	C D
0	C D
S	D

APPENDIX 6e. Results of Multiple Comparison LSD Test for H₂O_{leaf} (Leaf H₂O Mole Fraction)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	-3.960	-5.119 to -2.801	Yes	***	<.001	A-B
0 vs. B	0.3810	-0.7783 to 1.540	No	ns	.513	A-C
0 vs. BS	-1.466	-2.666 to - 0.2656	Yes	*	.018	A-D
0 vs. P	-0.8538	-2.013 to 0.3056	No	ns	.146	A-E
0 vs. PS	-3.700	-4.860 to -2.541	Yes	***	<.001	A-F
0 vs. PB	-3.662	-4.821 to -2.502	Yes	***	<.001	A-G
0 vs. PBS	-8.597	-9.757 to -7.438	Yes	***	<.001	A-H
S vs. B	4.341	3.182 to 5.500	Yes	***	<.001	B-C
S vs. BS	2.495	1.295 to 3.695	Yes	***	<.001	B-D
S vs. P	3.106	1.947 to 4.266	Yes	***	<.001	B-E
S vs. PS	0.2598	-0.8996 to 1.419	No	ns	.655	B-F
S vs. PB	0.2986	-0.8607 to 1.458	No	ns	.608	B-G
S vs. PBS	-4.637	-5.797 to -3.478	Yes	***	<.001	B-H
B vs. BS	-1.847	-3.047 to - 0.6466	Yes	**	.003	C-D
B vs. P	-1.235	-2.394 to - 0.07545	Yes	*	.037	C-E
B vs. PS	-4.081	-5.241 to -2.922	Yes	***	<.001	C-F
B vs. PB	-4.043	-5.202 to -2.883	Yes	***	<.001	C-G
B vs. PBS	-8.978	-10.14 to -7.819	Yes	***	<.001	C-H
BS vs. P	0.6118	-0.5882 to 1.812	No	ns	.311	D-E
BS vs. PS	-2.235	-3.435 to -1.035	Yes	***	<.001	D-F
BS vs. PB	-2.196	-3.396 to - 0.9959	Yes	***	<.001	D-G
BS vs. PBS	-7.132	-8.332 to -5.932	Yes	***	<.001	D-H
P vs. PS	-2.847	-4.006 to -1.687	Yes	***	<.001	E-F
P vs. PB	-2.808	-3.967 to -1.648	Yes	***	<.001	E-G
P vs. PBS	-7.744	-8.903 to -6.584	Yes	***	<.001	E-H

PS vs. PB	0.03887	-1.120 to 1.198	No	ns	.947	F-G
PS vs. PBS	-4.897	-6.056 to -3.738	Yes	***	<.001	F-H
PB vs. PBS	-4.936	-6.095 to -3.777	Yes	***	<.001	G-H
Compact letter display						
PBS	A					
S	B					
PS	B					
PB	B					
BS	C					
P	C D					
0	D E					
B	E					

APPENDIX 6f. Results of Multiple Comparison LSD Test for T_{leaf} (Leaf Temperature)

Uncorrected Fisher's LSD	Mean Diff.	95.00% CI of diff.	Below threshold?	Summary	Individual P Value	
0 vs. S	-1.878	-2.381 to -1.374	Yes	***	<.001	A-B
0 vs. B	0.1117	-0.3915 to 0.6150	No	ns	.658	A-C
0 vs. BS	-0.7622	-1.283 to -0.2413	Yes	**	.005	A-D
0 vs. P	-0.4596	-0.9628 to 0.04359	No	ns	.073	A-E
0 vs. PS	-1.724	-2.227 to -1.221	Yes	***	<.001	A-F
0 vs. PB	-1.707	-2.210 to -1.203	Yes	***	<.001	A-G
0 vs. PBS	-3.730	-4.233 to -3.227	Yes	***	<.001	A-H
S vs. B	1.989	1.486 to 2.492	Yes	***	<.001	B-C
S vs. BS	1.115	0.5944 to 1.636	Yes	***	<.001	B-D
S vs. P	1.418	0.9147 to 1.921	Yes	***	<.001	B-E
S vs. PS	0.1534	-0.3498 to 0.6566	No	ns	.544	B-F
S vs. PB	0.1710	-0.3322 to 0.6742	No	ns	.499	B-G
S vs. PBS	-1.853	-2.356 to -1.349	Yes	***	<.001	B-H
B vs. BS	-0.8739	-1.395 to -0.3531	Yes	**	.001	C-D
B vs. P	-0.5714	-1.075 to -0.06816	Yes	*	.027	C-E
B vs. PS	-1.836	-2.339 to -1.333	Yes	***	<.001	C-F
B vs. PB	-1.818	-2.321 to -1.315	Yes	***	<.001	C-G
B vs. PBS	-3.842	-4.345 to -3.339	Yes	***	<.001	C-H
BS vs. P	0.3026	-0.2183 to 0.8235	No	ns	.249	D-E
BS vs. PS	-0.9619	-1.483 to -0.4410	Yes	***	<.001	D-F

BS vs. PB	-0.9443	-1.465 to -0.4234	Yes	***	<.001	D-G
BS vs. PBS	-2.968	-3.489 to -2.447	Yes	***	<.001	D-H
P vs. PS	-1.265	-1.768 to -0.7613	Yes	***	<.001	E-F
P vs. PB	-1.247	-1.750 to -0.7437	Yes	***	<.001	E-G
P vs. PBS	-3.270	-3.774 to -2.767	Yes	***	<.001	E-H
PS vs. PB	0.01762	-0.4856 to 0.5208	No	ns	.944	F-G
PS vs. PBS	-2.006	-2.509 to -1.503	Yes	***	<.001	F-H
PB vs. PBS	-2.024	-2.527 to -1.520	Yes	***	<.001	G-H

**Compact
letter display**

PBS	A
S	B
PS	B
PB	B
BS	C
P	C D
0	D E
B	E