

UNIVERSIDAD AUTÓNOMA AGRARIA ANTONIO NARRO
SUBDIRECCIÓN DE POSTGRADO



APLICACIÓN DE NANOMATERIALES DE CARBONO Y SU EFECTO COMO
BIOESTIMULANTE EN TOMATE BAJO ESTRÉS SALINO

Tesis

Que presenta ELSY RUBISELA LÓPEZ VARGAS
como requisito parcial para obtener el Grado de
DOCTOR EN CIENCIAS EN AGRICULTURA PROTEGIDA

Saltillo, Coahuila

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Saltillo, Coahuila

Julio 2021

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Tesis

Elaborada por ELSY RUBISELA LÓPEZ VARGAS como requisito parcial para
obtener el grado de Doctor en Ciencias en Agricultura Protegida con la supervisión y

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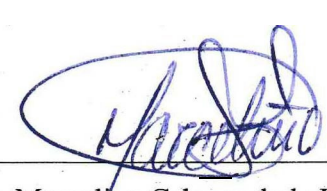
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Es para mí de gran satisfacción poder dedicar este trabajo con amor y cariño:

A Dios

A mis padres

A mis hermanos

A mi esposo y mi hija

Y a todos mis familiares y amigos que me brindaron su apoyo incondicional, gracias por confiar en mí, por ser parte de mi vida y permitirme ser parte de su orgullo.

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INTRODUCCIÓN

Actualmente, los principales desafíos que enfrenta la agricultura mundial incluyen el cambio climático, la urbanización, los problemas ambientales como la sequía, salinidad de agua y suelos, y la acumulación de pesticidas y fertilizantes (Fayaz et al., 2021). Estos problemas se intensifican aún más por un aumento alarmante de la demanda de alimentos que se necesitará para alimentar a una población mundial estimada para 2050 de 9.700 millones y de 10.900 millones para 2100 y, en consecuencia, la necesidad de desarrollar técnicas innovadoras para mejorar la productividad agrícola (Tommonaro et al., 2021).

La salinidad es sin duda una de las mayores limitaciones que influyen en el crecimiento y desarrollo de las plantas en todo el mundo, afectando el rendimiento y la productividad de diversos cultivos agrícolas (Benazzouk et al., 2020). Las sales solubles presentes en el suelo salino inducen estrés osmótico e iónico, lo que dificulta la adquisición de agua en las células vegetales y una deficiencia de nutrientes (Sadder et al., 2021). El estrés iónico perturba el equilibrio de las especies reactivas de oxígeno (ROS) en las células de las plantas, lo que causa directamente un estrés oxidativo (Baz et al., 2020). Sin embargo, las plantas son inherentemente dinámicas y flexibles, lo que les permite adaptarse y adquirir recursos para activar ciertos mecanismos y contrarrestar el estrés salino (Arsova et al., 2019). Los principales mecanismos incluyen cambios que ocurren a nivel morfológico, bioquímico, fisiológico y de desarrollo. Los mecanismos bioquímicos comprenden la homeostasis de ROS, un incremento en el sistema de defensa antioxidante, así como la activación de vías de eliminación de ROS, compartimentación de iones tóxicos, biosíntesis de osmolitos, homeostasis de iones, cambio en parámetros fotosintéticos y cambios hormonales (Kashyap et al., 2020).

En este contexto, los avances de la nanotecnología proporcionan herramientas novedosas para mejorar el sector agroalimentario, aquí destacan los nanomateriales (NMs) que en los últimos años se han empleado para la nanorremediación del suelo y el agua (Sharma et al., 2021), la nanonutrición de los cultivos (Seleiman et al., 2021), la nanoprotección de los cultivos (Adeel et al., 2021b), la mitigación de estreses bióticos o abióticos (Ors et al., 2021), además, se ha demostrado que pueden mejorar la absorción de agua y nutrientes (Zulfiqar y Ashraf, 2021). Algunos autores denominan a los NMs como “balas mágicas”

que alivian tensiones ambientales (Mahto et al., 2021), en especial a los nanomateriales de carbono (CNMs) debido a su biocompatibilidad y naturaleza ecológica, así como su fácil modificación de superficie, lo que aumenta su espectro de aplicación en la agricultura (Zaytseva and Neumann, 2016). Los NMs pueden ofrecer nuevas soluciones para una agricultura más eficiente y respetuosa con el medio ambiente al actuar como bioestimulantes e inducir una mayor tolerancia al estrés ambiental y mejorar la calidad nutracéutica de los alimentos (Juárez-Maldonado et al., 2018) por lo que la sostenibilidad agrícola es prometedora (Marella et al., 2021).

Los NMs tienen propiedades ópticas, térmicas, eléctricas y químicas específicas que les otorgan características específicas en comparación con sus contrapartes a granel, y se definen como materiales que poseen al menos una de las dimensiones externas o estructura interna dentro del rango de tamaño de 1 a 100 nm (Pramanik et al., 2020). Los NMs pueden activar el sistema de defensa de las plantas, a través de la formación de especies reactivas de oxígeno (Abdel Latef et al., 2017). Este sistema de defensa incluye la producción y acumulación de varios compuestos antioxidantes que participan en la tolerancia al daño causado por el estrés oxidativo (Tanveer et al., 2020). Dado que el estrés abiótico induce estrés oxidativo por la producción de ROS, es posible reducir estos daños por la producción de diferentes compuestos antioxidantes e inducir un incremento de la actividad enzimática que permita a la planta tolerar la salinidad (Pérez-Labrada et al., 2020).

Actualmente, estos NMs pueden clasificarse en nanopartículas metálicas (NPs) y CNMs; éstos últimos incluyen nanotubos de carbono (CNT) de pared simple (SWCNT), nanotubos de carbono de paredes múltiples (MWCNT), grafeno (GR) y fullerenos (Abd-Elsalam, 2020). Las características únicas de los CNMs han atraído gran atención en el campo agrícola debido a sus propiedades químicas y físicas y a la capacidad de translocación que depende del tamaño y la carga superficial de los mismos (carga negativa), promoviendo una serie de respuestas fisiológicas y bioquímicas que mejoran el crecimiento de la planta y la protección de los cultivos (Samadi et al., 2021).

Los CNT tienen una estructura tubular hecha de una o varias capas de átomos de carbono (láminas grafénicas) enrolladas entre sí, sus paredes forman una red hexagonal y sus extremos pueden ser abiertos o cerrados por una tapa semi hemisférica con forma de

fullereno (Shoala, 2020). Poseen la capacidad para penetrar las raíces y luego traslocarse hacia los haces vasculares y a la parte aérea por medio del xilema a través del flujo de transpiración (Zia-ur-Rehman et al., 2018), penetran la pared de las células, así como su membrana por medio de poros o canales por la vía apoplástica y por la vía de endocitosis, de esta manera se puede suministrar sustancias o productos químicos al interior de las células (Burman y Kumar, 2018; Khodakovskaya et al., 2009). Mientras que el GR es una estructura cristalina de grafito bidimensional plana atómica (2D) semejante a una red de panal de abejas y es un componente básico para los demás CNMs, una sola capa de grafeno enrollada en un cilindro conforma los SWCNT, mientras que los MWCNT consisten en dos o más envolturas cilíndricas concéntricas de láminas de grafeno (Rafiei, 2015). El GR tiene excelentes propiedades electrónicas, ópticas, mecánicas y térmicas (Radhakrishnan and Mathiyarasu, 2018), sin embargo, se ha demostrado ser tóxico para una variedad de especies, incluyendo vertebrados, algas, bacterias y hongos (Chen et al., 2018), y en altas dosis en plantas terrestres cultivadas hidropónicamente y expuestas a concentraciones de 0 a 2000 mg L⁻¹ (Begum et al., 2011).

El tomate es una de las hortalizas más importantes en el mundo, es de las de mayor demanda y mayor valor económico (Benazzouk et al., 2020). De igual manera, el fruto de tomate se ha identificado como un alimento funcional y nutraceutico, al ser una fuente importante de compuestos bioactivos tales como vitaminas, carotenoides y compuestos fenólicos, los cuales tienen gran actividad antioxidante que representa beneficios directos a la salud humana (Muzolf-Panek et al., 2017). Sin embargo, el cultivo es altamente sensible al estrés por salinidad, ya que la germinación, el crecimiento vegetativo, la formación de la fruta, el desarrollo, la maduración de la fruta y la calidad de la fruta se ven afectados por el alto contenido de sales en el suelo (Vaishnav et al., 2020).

Estudios recientes han demostrado que una exposición previa a un estrés leve prepara a las plantas contra eventos de estrés posteriores, por lo que los NMs aplicados con una dosis óptima pueden actuar como elicitores y preparar a la planta al activar su sistema de defensa y contrarrestar los efectos negativos causados por las tensiones ambientales (Kamanga et al., 2020).

En este contexto, se llevó a cabo el cebado de semillas de tomate con diferentes concentraciones de nanotubos de carbono y grafeno, con el objetivo de documentar las respuestas agronómicas y bioquímicas de plantas de tomate y sometidas a estrés salino.

REVISIÓN DE LITERATURA

Antecedentes

El término “nanotecnología” en el mundo científico fue formulado y usado por primera vez por el científico japonés Taniguchi en 1974. Según su definición, “la nanotecnología consiste principalmente en el procesamiento, separación, consolidación y deformación de materiales por un átomo o una molécula” (Sudha et al., 2018).

Dentro de la nanotecnología, existen materiales ya sea manufacturados o de forma natural con dimensiones a nanoescala denominados NMs. En un principio, los NMs se describían como materiales con longitud de 1 a 1000 nm en al menos una dimensión, sin embargo, hoy en día, existen varios textos legislativos en donde comúnmente se definen con un diámetro en el rango de 1 a 100 nm (Jeevanandam et al., 2018).

El uso de los NMs, se remonta a los siglos XIV y XIII a.C., en las antiguas regiones geográficas del imperio romano, cuando los egipcios y mesopotámicos comenzaron a fabricar vidrio utilizando metales para decoraciones. Al estudiar éstas decoraciones, se observaron propiedades ópticas asombrosas debido a la existencia de NPs como Ag y/o Cu. (Sudha et al., 2018).

Pero fue hasta la década de los 90's, cuando se lograron grandes avances en la investigación de materiales a nanoescala y la explotación de sus propiedades. En especial, en el descubrimiento del fullereno (C60) a finales de 1985 por Harry Kroto, en donde también se sintetizó CNT a base de fullerenos (Shoala, 2020). Sin embargo, los CNT se describieron realmente en 1991, por el investigador japonés Sumio Iijima, quien describe que los CNT generalmente tienen una forma cilíndrica, pero también se pueden presentar como diamantes, grafito o tubos, que son los diferentes alótropos del carbono (Irshad et al., 2020).

En el siglo XXI, la nanotecnología tiene una multitud de aplicaciones tecnológicas, biomédicas, farmacológicas o de ingeniería y es la tecnología con más potencial. En el sector agrícola, los NMs se pueden emplear para mejorar el crecimiento de las plantas de diferentes cultivos, mejorar el rendimiento de pesticidas y fertilizantes, así como aliviar los efectos negativos de los estreses bióticos y abióticos (Abd-Elsalam, 2020).

Salinidad en cultivos agrícolas

En la actualidad, la productividad agrícola enfrenta varios desafíos que incluyen el estrés biótico y abiótico (Mahto et al., 2021). El estrés abiótico conduce a una serie de cambios morfológicos, fisiológicos, bioquímicos y moleculares que afectan negativamente al crecimiento y la productividad de las plantas (Ors et al., 2021). Aproximadamente el 70% de la reducción del rendimiento de los cultivos está directa o indirectamente influenciada por el estrés abiótico (Mujtaba et al., 2021). La sequía, la salinidad y las temperaturas extremas son algunas de las tensiones abióticas más frecuentes, siendo la salinidad la que está presente durante todo el ciclo biológico de la planta por lo que induce limitaciones osmóticas e iónicas que reducen drásticamente el rendimiento en las especies cultivadas (Sadder et al., 2021) y amenazan la seguridad alimentaria mundial (Hamada y Hamada, 2020).

Alrededor del 10% del área total de suelo (950 Mha) y el 50% del área total de suelo bajo riego (230 Mha) del mundo está afectada por la salinidad (Zahedi et al., 2019). Este daño se debe a causas naturales y antropogénicas que incluyen una mayor evaporación relacionada con el cambio climático, riego con agua salina y malas prácticas agrícolas. Más del 6% de la superficie terrestre total del mundo está salinizada, y este porcentaje es mayor (alrededor del 25%) en las zonas áridas o semiáridas de la Tierra (Gandullo et al., 2021).

La salinidad de un suelo se mide en términos de conductividad eléctrica (CE), en unidades de dS m^{-1} ($1 \text{ dS m}^{-1} = 1000 \mu\text{S cm}^{-1}$) o mmhos cm^{-1} (equivalente a 1 dS m^{-1} o 1 mS cm^{-1}) y estos suelos tienen una mezcla de sales de sulfato, sodio, magnesio, cloro y calcio (Onyekachi et al., 2019). Al respecto, las sales que pueden inducir salinidad son NaCl , Na_2SO_4 , MgSO_4 , CaSO_4 , MgCl_2 , KCl y Na_2CO_3 , siendo el NaCl la sal más prevalente y de mayor efecto derivado de su disociación en Na^+ y Cl^- (Munns et al., 2019). Por lo tanto, la productividad de las plantas sensibles a la salinidad disminuye si la CE del suelo supera los 4 mS cm^{-1} ($4000 \mu\text{S cm}^{-1}$), por lo que se recomienda que el agua de riego no supere los 2 mS cm^{-1} (Hernández-Hernández et al., 2018b), ya que la mayoría de las especies de cultivos son sensibles al estrés salino (Godoy et al., 2021).

El estrés salino provoca un impacto negativo en varios procesos bioquímicos y fisiológicos, debido al aumento en la formación de ROS o especies reactivas de nitrógeno

(RNS) (Kumari et al., 2021), derivado del estrés iónico, osmótico y oxidativo sobre el metabolismo de las plantas (Pereira et al., 2021). Además, la salinidad provoca pérdida de contenido de agua y turgencia de las células de las hojas, una reducción de la fotosíntesis (destrucción del aparato fotosintético), deterioro del transporte de electrones, cierre estomático, toxicidad iónica y disminución del crecimiento celular (Fricke, 2020). Sin embargo, las plantas tienen mecanismos para contrarrestar el estrés salino. Estos mecanismos incluyen una homeostasis de ROS, un incremento en el sistema de defensa antioxidante, así como la activación de vías de eliminación de ROS, compartimentación de iones tóxicos, biosíntesis de osmolitos, así como una homeostasis de iones (Munns et al., 2019).

Por otro lado, la compartimentación de iones tóxicos se da mediante el transporte de sodio (Na^+), este mecanismo incluye la exclusión de Na^+ de la célula, o su inclusión en la vacuola y la compartimentación intracelular y la adquisición de potasio (K^+), ion que mantiene la homeostasis iónica de la célula, el potencial de la membrana, la fotosíntesis y la activación enzimática para hacer frente al estrés osmótico durante diferentes etapas de desarrollo del crecimiento de las plantas (Kumari et al., 2021).

Cabe mencionar que los mecanismos que utilizan las plantas para mitigar el estrés salino tienen un gasto energético muy elevado. Como la salinidad interfiere significativamente con los procesos metabólicos, el presupuesto de energía disminuye y con el tiempo se excede la capacidad de las células para mantener los iones tóxicos fuera del volumen del citoplasma, por lo que la concentración de Na^+ y Cl^- en el citoplasma crece de tal manera que provoca la muerte de las células (Fricke, 2020; Gandullo et al., 2021).

Especies reactivas de oxígeno

Las plantas se enfrentan constantemente a factores externos como la salinidad, sequía, altas y bajas temperaturas, entre otros; éstos factores tienen el potencial para promover la generación de ROS en el tejido vegetal, cuya acumulación dentro de la célula provoca un estrés oxidativo (Hasanuzzaman et al., 2019). La principal fuente de ROS en las plantas es la fotosíntesis, precisamente, en la cadena de transporte de electrones y la fotorrespiración en los peroxisomas, por lo que se forman principalmente en cloroplastos,

mitocondrias, membranas plasmáticas, peroxisomas, apoplasto y retículo endoplásmico (Zandalinas y Mittler, 2018).

Los ROS son el grupo más vital dentro de las especies reactivas, e incluyen radicales libres y formas no radicales. Entre los radicales libres se encuentran el anión superóxido ($O_2^{\cdot-}$), hidroxilo ($\cdot OH$) y el radical peroxilo (ROO^{\cdot}) y los no radicales, como el peróxido de hidrógeno (H_2O_2), oxígeno singlete (1O_2) y ozono (O_3) (Maurya, 2020).

El $O_2^{\cdot-}$ es generado en la membrana mitocondrial, se difunde hacia el genoma mitocondrial y reduce los metales de transición dentro del mismo genoma. El 1O_2 tiene propiedades aproximadamente equivalentes a las del $O_2^{\cdot-}$, solo que con mejor afinidad por los residuos de proteínas. El H_2O_2 está asociado con el inicio de estrés en las plantas y puede reaccionar con ADN y residuos de proteínas. Mientras que el $\cdot OH$ es extremadamente reactivo debido a su corta vida, potencial redox muy positivo y alta afinidad por biomoléculas, oxida de forma no selectiva ADN, proteínas, lípidos, aminoácidos, azúcares y metales, que provocan daños o inestabilidad genética (Dmitrieva et al., 2020).

No obstante, las ROS son reconocidas por desempeñar un papel doble, tanto perjudicial como beneficioso, dependiendo de su concentración en las plantas (Carvalho y Silveira, 2020). Pueden actuar como moléculas de señalización implicadas en procesos como el crecimiento, el ciclo celular, el desarrollo, la senescencia, la muerte celular programada, la conductancia estomática, la señalización hormonal y la regulación de la expresión génica (Hussain et al., 2021).

Mecanismos de defensa antioxidante

Los estreses bióticos o abióticos generan numerosos efectos perjudiciales que conducen al estrés oxidativo, debido a una sobreacumulación de ROS en las plantas. Sin embargo, las plantas son organismos dinámicamente flexibles y tienen vías de eliminación o sistemas de desintoxicación bien desarrollados para contrarrestar los efectos deletéreos de las ROS (Ali y Mujeeb-Kazi, 2021).

Los sistemas de defensa antioxidantes de las plantas incluyen compuestos enzimáticos y no enzimáticos, los cuales son moléculas capaces de inhibir o apagar las reacciones de los radicales libres y retrasar o prevenir el daño celular (Dumanović et al., 2021), por ello se consideran la primera línea de defensa celular contra las ROS (Sies y Jones, 2020). Éstos

compuestos antioxidantes se encuentran ubicados en diferentes compartimentos celulares, en particular, como isoformas que existen en las mitocondrias, cloroplastos y peroxisomas que facilitan la captación de las ROS (Kashyap et al., 2020).

Compuestos antioxidantes no enzimáticos

Dentro de los antioxidantes no enzimáticos se encuentran el ácido ascórbico o vitamina C (AsA), glutatión (GSH), alcaloides, carotenoides (licopeno y β -caroteno), flavonoides, compuestos fenólicos y tocoferoles (Pérez-Labrada et al., 2019).

El AsA es un potente antioxidante que protege a las plantas del daño oxidativo, al actuar como un sustrato en las reacciones catalizadas por la enzima ascorbato peroxidasa (APX) reduciendo el H_2O_2 en agua (H_2O), además, tiene la capacidad de donar electrones, lo que le permite actuar directamente como un antioxidante al secuestrar las ROS (Sakhno et al., 2019).

Los carotenoides como el licopeno, β -caroteno, xantofilas, luteínas y zeaxantinas, son antioxidantes lipofílicos capaces de evitar la formación o eliminación de 1O_2 por el ciclo de las xantofilas y capturar con mayor eficacia el radical lípido peroxilo (LOO^\bullet) (Hussain et al., 2019). Además, funcionan como moléculas de antena, al capturar la luz en los cloroplastos. En particular, el licopeno, tiene 11 enlaces dobles conjugados, lo que lo convierte en uno de los neutralizadores de 1O_2 más eficientes entre los carotenoides naturales, debido a que la eficacia de la actividad antioxidante está en función de la velocidad de recuperación de su estado básico y del número de sus dobles enlaces (Dumanović et al., 2021). El papel principal del β -caroteno en los tejidos verdes es la extinción de $^3Chl^*$, proporcionando así la inhibición de la producción y el daño de 1O_2 , además de que participa en la formación de la provitamina A (Szymanska et al., 2014).

El GSH protege a las plantas del daño oxidativo, eliminando H_2O_2 , 1O_2 , OH^\bullet y $O_2^{\bullet-}$. Sin embargo, el papel principal del GSH como antioxidante es su capacidad para regenerar el ácido ascórbico a través del ciclo AsA-GSH (Chen et al., 2017). Además, desempeña funciones importantes en varios procesos biológicos, incluido el crecimiento celular, el desarrollo, la regulación del transporte de azufre, la transducción de señales, la síntesis de proteínas y ácidos nucleicos, la síntesis de fitoquelatina para la quelación de metales,

desintoxicación de xenobióticos y expresión de genes responsables del estrés (Tuzet et al., 2019).

Los compuestos fenólicos, incluidos los flavonoides, son antioxidantes que desencadenan una serie de metabolitos secundarios sintetizados a partir de la vía del ácido shikímico o por la vía de los fenilpropanoides (Filippis, 2016). Éstos compuestos pueden eliminar radicales libres, especialmente $O_2^{\cdot-}$, $\cdot OH$, ROO^{\cdot} , debido a su alta reactividad como donantes de electrones. Su capacidad antioxidante está relacionada con su estructura (anillo aromático con sustituyentes $-OH$ o $-OCH_3$), adecuada para atrapar radicales libres (Gutiérrez-Grijalva et al., 2018). Además, capturan directamente 1O_2 e inhiben la peroxidación de lípidos atrapando radicales alcoxi de lípidos. Mientras que los flavonoides son compuestos de bajo peso molecular y, especialmente, las flavonas y flavonoles dihidroxi sustituidos con anillo B tienen un gran potencial para eliminar los radicales libres y reducir el daño celular de la peroxidación (Mathesius, 2018).

Compuestos antioxidantes enzimáticos

En el sistema enzimático, se incluyen enzimas de defensa antioxidantes como catalasa (CAT), peroxidasa (POD), peroxiredoxina (PRX), glutatión peroxidasa (GPX), superóxido dismutasa (SOD), ascorbato peroxidasa (APX), monoenzimas deshidroascorbato reductasa (MDAR), y proteínas similares a la nicotinamida adenina dinucleótido fosfato (NADPH), entre otras (Hermes et al., 2020).

La enzima SOD pertenecen a la familia de metaloenzimas y su función principal es actuar como primera línea de defensa al convertir el $O_2^{\cdot-}$ en H_2O_2 . De acuerdo a los cofactores metálicos (Cu, Zn, Mn o Fe) presentes en el sitio activo, las SOD se han categorizado en tres grupos Cu-ZnSOD, MnSOD y FeSOD en plantas que realizan una función específica dependiendo de su localización celular (Saibi y Brini, 2018). La CAT es una enzima tetramérica que convierte el H_2O_2 en H_2O y O_2 . Un aumento en la actividad CAT es dependiente de la concentración de H_2O_2 , por lo que existe una correlación entre los componentes de los sistemas de eliminación de ROS entre CAT y SOD (Tuzet et al., 2019). El APX elimina el H_2O_2 utilizando ascorbato como donante de electrones específico para reducir el H_2O_2 a H_2O , y juega un papel central en el ciclo de ascorbato-glutatión por lo que la inducción de APX es una respuesta al estrés oxidativo causado en

las plantas por estrés biótico o abiótico (Yan et al., 2016). GPX es una enzima antioxidante con una cisteína en su sitio activo, tienen una fuerte actividad contra el H_2O_2 , podrían usar tanto GSH como tioredoxina como sustratos reductores y eliminarán los peróxidos de lípidos además del H_2O_2 (Pérez-Labrada et al., 2019). Además de su papel en la neutralización de H_2O_2 , CAT y GPx junto con la enzima SOD muestran un efecto sinérgico en la eliminación de $O_2^{\cdot-}$ (Dumanović et al., 2021).

Importancia del cultivo de tomate

El tomate (*Solanum lycopersicum* L.) es una de las hortalizas más producidas y consumidas a nivel mundial. Es el segundo cultivo vegetal más importante desde el punto de vista agronómico después de la papa (*Solanum tuberosum* L.) (Kumari et al., 2021). En México es el tercer producto agrícola de exportación y una de las principales hortalizas exportadas, principalmente a Estados Unidos, por su proximidad geográfica, competitividad en precio, calidad y buen sabor (Flores et al., 2021).

Botánicamente, el tomate es una baya de fruta, pero debido a su amplio uso con fines culinarios, se trata como verdura, y es una de las verduras más bajas en calorías (18 kcal) con cero niveles de colesterol. El contenido de agua del tomate es de alrededor del 95% y los carbohidratos y la fibra constituyen el otro 5% (Kumari et al., 2021). Las características organolépticas de los tomates están relacionadas con su composición química, la cual incluye compuestos importantes como polifenoles, flavonoides, ácido fólico, carotenoides (β -carotenos y licopeno) y ácido ascórbico, también es una rica fuente de minerales como P, K, Ca, Mg, Na, Zn, Fe y B, vitaminas A y B, y ácidos orgánicos como el ácido cítrico, ácido málico, y el ácido glutámico, todos estos compuestos actúan como antioxidantes que ayudan a prevenir enfermedades cardiovasculares y cancerígenas (Flores et al., 2021; Sabbineni et al., 2021).

El tomate suprime la proliferación de células cancerosas, protege del cáncer de próstata, del tracto digestivo y de los trastornos cardiovasculares (Ali et al., 2021). El consumo de tomate aumenta significativamente los niveles de licopenos, carotenoides cutáneos totales, fitoflueno y fitoeno en suero humano que protege la piel contra el eritema inducido por la luz UV (Ilahy et al., 2019). El epicarpio del tomate contiene naringina, que reduce la inflamación, aterosclerosis, trastornos cardiovasculares, diabetes mellitus y actúa como

antioxidante. Además, los tomates también juegan un papel vital en la salud ósea con un aumento significativo en el crecimiento del fémur y la tibia (Kumari et al., 2021; Sabbineni et al., 2021).

El cultivo de tomate es sensible a niveles moderados de salinidad como la mayoría de las otras plantas de cultivo. La germinación de la semilla, el crecimiento vegetativo y las etapas reproductivas del tomate como la formación, el desarrollo, la maduración y la calidad de la fruta, muestran una alta sensibilidad al estrés salino, y el rendimiento económico se reduce drásticamente en estas condiciones (Sabbineni et al., 2021). La disminución en el crecimiento de la planta de tomate cuando se aplica NaCl al medio de crecimiento se atribuye a los mecanismos de estrés osmótico y estrés iónico, debido a que las grandes cantidades de Na^+ provocan un desequilibrio de nutrientes por la competencia entre el Na^+ y otros cationes, además de una acumulación de grandes cantidades de ROS responsables del estrés oxidativo (Amjad et al., 2019). Sin embargo, las plantas de tomate pueden desarrollar estrategias para tolerar este estrés mediante una cascada de interacciones complejas que ayudan a mitigar el daño causado por la salinidad (Kumari et al., 2021).

Nanotecnología en la agricultura

De acuerdo al constante crecimiento de la población mundial, se pronostica que se requerirá un aumento de entre el 60 y el 110% en la producción mundial de alimentos (Godoy et al., 2021). Sin embargo, la producción agrícola no aumenta a un ritmo paralelo, por lo que aumentar la productividad es uno de los mayores desafíos para la industria alimentaria (Sadder et al., 2021). Actualmente la nanotecnología juega un papel importante en la producción mundial de alimentos y seguridad alimentaria (Ashraf et al., 2021).

La aplicación de la nanotecnología en la agricultura ha sido un interés clave para el sector agrícola y los investigadores durante las últimas décadas (Jun et al., 2021). El potencial de la nanotecnología para generar cambios en la industria agrícola es prometedor. La invención de herramientas y equipos basados en nanotecnología tienen el objetivo de aumentar la eficiencia agrícola, así como superar los desafíos actuales (Hossain et al., 2020). Una de las herramientas que la nanotecnología ha desarrollado son los NMs, éstos

tienen un área superficial relativamente mayor en comparación con la misma masa de material producido en una forma más grande. Además, el tamaño de las partículas tiene una alta relación superficie/volumen que aumenta su reactividad y posible actividad bioquímica (Das et al., 2019).

Algunos NMs como metaloides y óxidos metálicos, además de quitosano, nanotubos de carbono, grafeno y fullerenol, han llamado mucho la atención, además de demostrar excelentes beneficios con su aplicación en diferentes campos del sector agrícola. Estas aplicaciones incluyen la nanorremediación del suelo y el agua (Sharma et al., 2021), la nanonutrición de los cultivos (Seleiman et al., 2021), la nanoprotección de los cultivos (Adeel et al., 2021b), la mitigación de estreses abióticos (Ors et al., 2021) y, por lo tanto, el logro de la sostenibilidad agrícola (Marella et al., 2021).

La adopción del uso de los NMs en la agricultura mejora la eficiencia y la sostenibilidad de las prácticas agrícolas al poner menos insumos y generar menos desechos que los productos y enfoques convencionales. En general se espera que los NMs aplicados en la agricultura puedan desempeñar un papel crucial para aumentar la producción agrícola y satisfacer las demandas de una población en crecimiento (Vedamurthy et al., 2021).

Nanomateriales en las plantas

La implementación directa de los NMs con las plantas implica la pulverización foliar y la administración en el suelo, mientras que la interacción indirecta puede implicar el uso de nanosensores para la detección de contaminantes de suelo (Pandey et al., 2021). Los efectos de los NMs en diferentes especies de plantas pueden variar mucho con las etapas de crecimiento de las plantas, el método y la duración de la exposición y dependen de la forma, tamaño, composición química, concentración, estructura de la superficie, agregación y solubilidad de los NMs (Bai et al., 2021).

Algunos NMs pueden diseñarse inspirándose en rutas transgénicas y naturales probadas para interactuar con la fotosíntesis y la fotoprotección, por ejemplo, al ser incorporados en las membranas de los tilacoides dentro de los cloroplastos, pueden incrementar el transporte de electrones en las hojas y los mismos cloroplastos, por lo que se obtiene un mayor rendimiento en la fotosíntesis lo que da como resultado un aumento y rendimiento de los cultivos (Giraldo et al., 2014).

De igual manera, los NMs pueden estimular el crecimiento de las plantas mediante efectos positivos sobre la germinación de semillas, el crecimiento de raíces o brotes, así como la producción de biomasa o grano (Zhao et al., 2020). La interacción de la célula vegetal con los NMs conduce a la modificación de la expresión de genes vegetales y las vías biológicas asociadas, que influyen el crecimiento y desarrollo de las plantas (Nakamichi et al., 2020). Algunos NMs se utilizan el cebado de semillas y tienen un impacto positivo en la mejora del crecimiento de las plantas (Baz et al., 2020; Ratnikova et al., 2015). Khodakovskaya et al. (2013), reportaron un incremento en la floración, mayor desarrollo de frutos y por lo tanto mayor rendimiento en plantas de tomate tratadas con NMs, esto debido a la expresión del gen de las acuaporinas. También se ha reportado un crecimiento más rápido y mejoras en el rendimiento en plantas de trigo (Joshi et al., 2018a) y arroz (Joshi et al., 2020), ambos estudios son el resultado de una mejor absorción de agua y minerales esenciales como P y K. El efecto de los NMs en la absorción de los nutrientes depende como se ha dicho anteriormente, de diversos factores como la especie vegetal, el tipo de nanomaterial, la forma de aplicación, entre otros, ya que se ha demostrado que el mismo nanomaterial pero de diferente tamaño tiene un efecto diferente en la misma planta o a su vez en plantas diferentes (Fayaz et al., 2021).

Por otro lado, los NMs ingresan a las células y pueden interactuar directamente con el material genético o pueden afectar moléculas intermedias indirectamente, lo que conduce a la producción de ROS o especies reactivas de nitrógeno (RNS) que causan estrés oxidativo y generan citotoxicidad, genotoxicidad, peroxidación de lípidos, apoptosis, degradación de proteínas intracelulares y desregulación de miARN (Rahmani et al., 2020). En este sentido, el uso de NMs en las plantas induce cambios en las plantas, el sistema de defensa antioxidante es una de las principales líneas que modifican su actividad para proteger a la planta ante un cambio no previsto (estrés) (Mahto et al., 2021). La alteración en la acumulación de proteínas bajo estrés por NMs está estrechamente relacionada con la respuesta fenotípica de la planta, ya que los cambios a nivel de transcripción no siempre coinciden con la alteración a nivel de proteína (Jha y Pudake, 2016). Además, los NMs pueden afectar directa o indirectamente las actividades metabólicas tanto del suelo como de las plantas. Las perturbaciones de los metabolitos en las plantas ocurren en respuesta

al nivel de estrés, y alteran principalmente el metabolismo de los carbohidratos, la energía, los aminoácidos, los lípidos y el metabolismo secundario (Li et al., 2019).

Absorción, transporte y translocación de nanomateriales

La acumulación y absorción de los NMs es diferente dependiendo del tipo de planta, composición química, tipo y tamaño de los NMs. Generalmente, hay dos rutas de exposición principales para las plantas con respecto a la absorción y translocación de los NMs: vías radicales o foliares (Du et al., 2017). Se ha demostrado que los NMs pueden ingresar a las células vegetales al unirse a una proteína transportadora, a través de acuaporina, canales iónicos o endocitosis a través de la creación de nuevos poros, entre otros (Aslani et al., 2014). Una vez dentro de la planta, pueden formar complejos con transportadores de membrana o exudados de raíces antes de ser transportados apoplásticamente o simplásticamente de una célula a otra a través de plasmodesmos y translocarse vía xilema o floema (Pérez-de-Luque, 2017).

En este sentido, las estructuras anatómicas como las raíces y las hojas de las plantas juegan un papel importante en la deposición de los diferentes NMs, y recientemente a través de las semillas (Ratnikova et al., 2015).

Absorción

○ **Semillas**

En las semillas, los NMs entran a través de la cubierta de la semilla (Khodakovskaya et al., 2009). Pueden entrar a través de espacios intercelulares parenquimatosos y llegar hasta el cotiledón. La regulación de NMs en los cotiledones está mediada por acuaporinas (Kumar et al., 2019). Diversos autores mencionan que a través de la imbibición, algunos NMs como los CNT pueden romper la capa dura de la semilla y crear poros para ingresar dentro de la semilla (Khodakovskaya et al., 2009; Ratnikova et al., 2015).

○ **Raíz**

La aplicación de los NMs en el suelo, permiten una bioacumulación en las raíces de las plantas, y se da por medio de la adsorción, y posteriormente mediante una absorción química o física sobre las plantas a través de la pared celular y la membrana plasmática

de las células de la raíz (Faisal et al., 2018). Éste proceso se lleva a cabo mediante una adhesión mecánica; sin embargo, esto depende de la especie de planta ya que unas adsorben más cantidades que otras, y a su vez del nanomaterial en cuestión ya que algunos pueden ser fácilmente adsorbidos por las raíces (Chen, 2018). Una alta absorción de NMs en las superficies de las raíces podría causar daños estructurales y comprometer la integridad celular. Ante esto, existe la posibilidad de que se agranden los poros o se induzcan nuevos poros en la pared celular tras la interacción con los NMs, como los CNT (Khodakovskaya et al., 2013). Éstos pueden perforar físicamente las paredes de las células epidérmicas y de las células ciliadas de la raíz, lo que altera la composición de los tejidos y facilita la entrada de los NMs en el citoplasma celular (Deng et al., 2017). Además, las raíces laterales recién formadas rompen la región cortical y permiten el flujo de derivación apoplástico y la entrada de NMs al xilema a través de la corteza hacia el cilindro central (Dev et al., 2018).

○ **Hojas**

Cuando los NMs son aplicados de manera foliar, éstos entran en contacto con la superficie de las hojas y pueden entrar a través de vías cuticulares y estomáticas o a través de las bases de los tricomas y luego trasladarse a varios tejidos a través del floema (Deng et al., 2014). La vía cuticular suele limitarse a los NMs con tamaños inferiores a 5 nm debido a los tamaños extremadamente pequeños de los poros cuticulares. Por otro lado, las vías estomáticas permiten la penetración de NP más grandes ya que el tamaño estomático típico está en un rango de tamaño micrométrico (Hasaneen et al., 2016).

✚ **Transporte**

Los NMs forman diferentes complejos con transportadores de membrana, exudado de raíces y se absorben de acuerdo a su forma de aplicación (foliar o suelo). Después de entrar en las células, se transportan de forma apoplástica o simplástica en el sistema vegetal (Burman y Kumar, 2018).

● **Vía apoplástica**

Este tipo de transporte, tiene lugar fuera de la membrana plasmática a través de los espacios extracelulares, las paredes celulares de las células adyacentes y los vasos del

xilema (Pérez-de-Luque, 2017). Cuando los NMs atraviesan paredes celulares porosas, las partículas pueden difundirse en el espacio entre la pared celular y la membrana plasmática, además, están sujetas a presión osmótica o fuerzas capilares (Kumar et al., 2019). Esta vía es importante para el movimiento radial dentro de los tejidos vegetales y permite que los NMs alcancen el cilindro central de la raíz y los tejidos vasculares, para un mayor movimiento hacia arriba de la parte aérea a través del xilema, siguiendo la corriente de transpiración (Banerjee et al., 2019). Sin embargo, al llegar al xilema existe una barrera denominada banda de caspary, que impide el paso de los NMs, y hace que se formen agregados y se acumulen en la endodermis, por lo que para una translocación eficaz a la parte aérea se debe continuar a través de la vía simplástica para penetrar en el sistema vascular (Deng et al., 2014).

- **Vía simplástica**

La ruta simplástica es la ruta más importante y altamente regulada para transportar los NMs a los cultivos. El transporte simplástico implica el movimiento de agua y sustancias entre el citoplasma de las células adyacentes a través de estructuras especializadas llamadas plasmodesmos (Kumar et al., 2019). La internalización celular de los NMs ocurre al unirse a proteínas transportadoras, a través de acuaporinas, canales iónicos, endocitosis o creando nuevos poros y a través de plasmodesmos (Khan et al., 2019). Los plasmodesmos conectan diferentes células vegetales y el transporte a través de las células se facilita fácilmente a través de este paso. El efecto hidrofóbico/hidrofílico puede alterar la interacción de los NMs con las membranas de las células vegetales. Los NMs hidrófobos tienden a incrustarse en el núcleo hidrófobo de la membrana sin que se produzcan fugas en la membrana; mientras que los NMs hidrófilos favorecen la adsorción en la superficie de la bicapa y es más probable que se unan a las vesículas intracelulares (Schwab et al., 2016).

Los NMs en el citoplasma pueden estar rodeados de proteínas u otras biomoléculas que forman una corona. Una vez dentro de las células, los endosomas que contienen NMs o el complejo NMs-proteína podrían someterse a un transporte eficiente a las células vecinas a través de plasmodesmos, que normalmente tienen un diámetro de 20 a 50 nm (Chetwynd y Lynch, 2020). Debido al alto volumen de material involucrado en el flujo simplástico,

esta vía puede resultar muy eficaz para el transporte de NMs a través de la endodermis y a los tejidos vasculares posteriores (Medina-Velo et al., 2017).

Hay muchos factores que pueden afectar la absorción y transporte de los NMs, por ejemplo, las plantas con baja transpiración, tolerancia a la sequía, arquitectura de pared celular resistente y crecimiento alto tienden a translocar menos NMs. También los pelos radiculares, la repelencia de las hojas, la porosidad de la membrana de la cutícula, la segmentación del xilema, las heridas, las raíces laterales, los nudos, la banda de Caspary, los hidátodos, las lenticelas y los tricomas pueden afectar la absorción de los NMs (Chichiricco y Poma, 2015). Además, la composición de la pared celular, el mucílago y los microorganismos simbióticos (micorrizas) en el suelo, la ausencia de una cutícula (plantas sumergidas), la apertura de los estomas, entre otros (Dev et al., 2017; Miralles et al., 2012; Montes et al., 2017).

Translocación

Las características tanto de los NMs como de las plantas juegan un papel importante en la translocación de los NMs (Chen, 2018). La translocación de NMs depende de la cantidad suministrada y de la naturaleza de la planta como especie (Aslani et al., 2014). Los NMs se mueven de las hojas a las raíces, el tallo y el grano o fruto en desarrollo, y de una raíz a otra. El mecanismo de translocación se inicia con la penetración de NMs a través de las paredes celulares y la membrana plasmática de las células de las hojas o raíz, dependiendo de la forma de aplicación del nanomaterial (Husen, 2020).

Uno de los principales canales de captación y transporte a los brotes y hojas de la planta es el xilema, y de las hojas a las raíces es el floema. Los NMs absorbidos por las raíces de las plantas pueden trasladarse a los brotes de las plantas u otros tejidos vegetales, incluidas las semillas de reciente desarrollo (Reddy et al., 2019). También se ha demostrado que no todas las NPs se trasladan en su forma prístina a los tejidos vegetales, ya que algunas al estar en contacto con otras sustancias del medio como los exudados de las raíces, el mucilago o componentes del citoplasma, se biotransforman, y como consecuencia favorecen o limitan su transporte a otras partes de la planta (Hernandez-Viezcas et al., 2013).

El xilema es uno de los principales pasajes de absorción y transporte al brote y las hojas de la planta. El tamaño de los poros de la pared celular (3 a 8 nm), es más pequeño que los NMs y la translocación de NMs a través de xilema depende principalmente de varios factores como la tasa de transpiración, la presión de las raíces, algunos factores ambientales como la temperatura, la humedad y la interacción carga-carga entre NMs y plantas (Husen, 2020).

El floema es otro mecanismo de transporte de los NMs a diversos órganos de la planta. Diversos estudios acerca de la captación de NMs ya sea raíz u hojas, demostraron que dichos NMs están distribuidos aleatoriamente en toda la planta, lo que sugiere que la translocación a través del floema puede estar más regulada y organizada que a través del xilema (Su et al., 2019a).

Algunos NMs se transportan principalmente a través del xilema y no del floema, por lo que se muevan de la raíz a los brotes y hojas, y no hacia abajo, y por lo tanto, para lograr una buena distribución la aplicación adecuada sería a la raíz. Por el contrario, existen otros NMs que se translocan a través del floema por lo que su aplicación debe realizarse por aspersión foliar, lo que indica que la forma, las dimensiones y la carga superficial de los NMs afectan su absorción ya sea por las raíces o las hojas de las plantas y su transporte hacia los órganos. En las raíces, los NMs con al menos una dimensión inferior a 50 nm presentan una mejor absorción y, los NMs inferiores a 28 nm presentan un mayor transporte desde las raíces hacia los brotes (Su et al., 2019a). Wang et al. 2012, encontraron que las NPs de CuO de 20 a 40 nm se trasladaron de las raíces del maíz a los brotes a través del xilema y luego de los brotes a las raíces a través del floema, mientras que Hong et al. 2014, demostraron la translocación hoja-raíz de NPs de CeO₂ en pepino, además, encontraron NPs de CeO₂ en otros tejidos no vasculares, indicando un transporte de floema.

Sin embargo, los NMs que se mueven a lo largo del floema probablemente se acumularán en los órganos de las plantas que actúan como sumideros, lo que genera una preocupación sobre la seguridad de los NMs, los niveles de exposición y las repercusiones toxicológicas en el medio ambiente y la salud humana (Singh et al., 2021).

Nanomateriales de carbono

Los CNMs cubren alrededor del 40% de todos los NMs artificiales utilizados para aplicaciones agrícolas (Abd-Elsalam et al., 2020; Mohamed et al., 2018). La familia de los CNMs incluye fullerenos, nanocuernos, puntos de carbono (CDs), CNT y grafeno (Jampílek y Králová, 2021). Todos ellos exhiben una gran diversidad en sus estructuras, así como en el tamaño, que no se limita exclusivamente a la nanoescala (<100 nm) en todas las dimensiones (Abd-Elsalam et al., 2020; Mohamed et al., 2018). Durante el tiempo relativamente corto desde el descubrimiento de los fullerenos en 1985, los nanotubos de carbono en 1991 y el grafeno en 2004, las propiedades únicas de los CNMs han atraído un gran interés, lo que ha promovido el desarrollo de métodos para la producción industrial a gran escala, así como su aplicación en diferentes áreas de interés farmacéutico, industrial, agrícola, entre otros (Aacharya y Chhipa, 2020).

En comparación con otros NMs a base de metales, los CNMs muestran una toxicidad medioambiental mucho menor y una mayor biocompatibilidad debido a su estructura de carbono no tóxica, además, pueden degradarse en el medio ambiente y los cambios fisicoquímicos derivados modifican su toxicidad original. (Li et al., 2020). Li et al. 2018, demostraron que los CDs, aplicados en arroz, pueden degradarse en productos que tienen las características y estructuras básicas comunes de hormonas vegetales, que la planta podría considerar como análogos de las mismas para promover el crecimiento. También, los CDs al degradarse, pueden formar CO₂, el cual se puede convertir en carbohidratos a través del ciclo de fotosíntesis de Calvin.

En la actualidad, la degradación de los CNMs se divide principalmente en dos categorías, degradación química y biodegradación. La biodegradación incluye la degradación celular, la degradación enzimática y la degradación bacteriana, siendo la degradación enzimática la más estudiada. Además, se ha demostrado que los CNMs se pueden biodegradar en el entorno natural mediante una catálisis enzimática. El estudio de la degradabilidad de los CNMs ayuda a mejorar la seguridad de su aplicación en el medio ambiente (Peng et al., 2020).

Diversos estudios han evaluado el efecto de los CNMs en diversos cultivos agrícolas de interés comestible e industrial. Los resultados han reportado efectos positivos que van desde el mejoramiento en la germinación de semillas hasta el incremento en la

productividad y el rendimiento de los cultivos. Además, los CNMs producen respuestas morfológicas, fisiológicas y bioquímicas que ayudan a la planta a tolerar algún tipo de estrés ya sea biótico o abiótico y de igual manera se ha reportado que el uso de los CNMs en las plantas genera cambios en el transcriptoma, proteoma, metaboloma e ionoma (González-Morales et al., 2020).

Nanotubos de carbono

Los CNT, son nanoestructuras tubulares únicas, que difieren en diámetro, longitud, número de capas y quiralidad. Según la estructura, los CNT se pueden dividir en dos categorías principales: SWCNT y MWCNT. En general, los SWCNT tienen alrededor de 1 a 3 nm de diámetro y una longitud de unos pocos micrómetros, mientras que los MWCNT tienen entre 5 y 40 nm de diámetro y una longitud de aproximadamente 10 micrómetros (Bhalla et al., 2021). Los SWCNT consisten en una sola capa de grafeno y los MWCNT comprenden una capa de múltiples capas de grafeno (Patel et al., 2020). En la agricultura, ha habido un gran interés en el uso de CNT. Sin embargo, la literatura revela los efectos mixtos de la exposición a CNT en las plantas, aumentando el rendimiento de los cultivos por un lado, mientras que causa citotoxicidad aguda en plantas (Rudakiya et al., 2019).

- **SWCNT**

Los SWCNT actúan como nanotransportadores para transferir ADN y moléculas de colorante a las células de las plantas. Además, tienen una capacidad de afectar de manera benéfica o perjudicial la germinación de las semillas y el crecimiento de las plantas al inducir la eficiencia de absorción de agua y nutrientes que da como resultado una mejora en la raíz y el tallo (Ioannou et al., 2020). En un estudio realizado por Joshi et al., (2020) evaluaron SWCNT (1 y 10 mg kg⁻¹) en plantas de tomate y reportaron que la a exposición a SWCNT aumentó significativamente el contenido de ácido salicílico (SA) por lo que los SWCNT pueden provocar una respuesta al estrés. Por otro lado, Hatami et al., (2018) expusieron semillas de *Hyoscyamus niger* L. con SWCNT (50-800 µg ml⁻¹) bajo diferentes niveles de estrés por sequía (0.5-1.5 MPa). Los resultados demostraron que con concentraciones bajas de SWCNT se puede inducir tolerancia en las plántulas contra

niveles de sequía bajos mediante la mejora de la absorción de agua y la activación del sistema de defensa de la planta (SOD, POD, CAT y APX) así como la biosíntesis de proteínas, fenólicos y metabolitos específicos como la prolina. También se observó una reducción en los índices de daño oxidativo, incluido el H_2O_2 , el contenido de malondialdehído y la fuga de electrolitos.

- **MWCNT**

Diversos estudios reportan que los MWCNT son productos ideales para aumentar la calidad del rendimiento de las plantas, a través del uso de los nanofertilizantes, nanopesticidas y nanoherbicidas. Los MWCNT pueden incrementar la formación de especies reactivas de oxígeno, y a su vez incrementar el sistema de defensa de las plantas mediante la modificación de compuestos antioxidantes enzimáticos y no enzimáticos (Samadi et al., 2020). También se ha reportado que niveles bajos de MWCNT (50 y 100 mg L^{-1}) pueden incrementar el diámetro del xilema y floema en la raíz, así como el tamaño de los estomas y el índice estomático de las hojas, lo que les confiere a las plantas una mejora en la actividad fotosintética y un mayor flujo de nutrientes en el sistema vascular (Jamei et al., 2020). Algunos estudios afirman que los CNT de más de 200 nm se acumulan en orgánulos subcelulares, mientras que los nanotubos más pequeños (30-100 nm) pueden penetrar la vacuola y el núcleo (Paramo et al., 2020), además, los CNT de menor tamaño pueden ser nanotransportadores de genes (ADN / ARN / ARNip y proteínas) para desarrollar y establecer una expresión genética transitoria en células vegetales en todo tipo de especies en comparación con los métodos existentes (Chandrasekaran et al., 2020).

Por otra parte Cao et al., (2020) mencionan que los MWCNT influyen en la formación de raíces laterales (LR), esto fue demostrado al aplicar MWCNT (0, 0.05, 0.5, 5 y 50 mg ml^{-1}) en plántulas de tomate de una forma dependiente de la dosis. Además, observaron que existe una relación de causa-efecto entre MWCNT y óxido nítrico (NO) en la inducción del desarrollo de LR al incrementar la actividad de la enzima nitrato reductasa (NR) (generadora de NO) en respuesta a los MWCNT. Los autores concluyeron que el NO podría actuar como una molécula de señalización para el desarrollo de LR, al menos parcialmente a través de la NR. Joshi et al., (2018) aplicaron MWCNT (90 $\mu\text{g ml}^{-1}$) en avena mediante el método de cebado de semillas y observaron que estos NMs entran en

la planta y atraviesan las células. Así mismo, la presencia de MWCNT dentro de la avena mejoró el crecimiento de las células del xilema en aproximadamente 1.85 veces. También aumentó el contenido de clorofila en un 57%, mientras que la actividad fotosintética aumentó en un 15% y por ende obtuvieron un mejor rendimiento. Pandey et al., (2018) evaluaron el impacto MWCNT (50 y 200 $\mu\text{g ml}^{-1}$) en la germinación y producción de biomasa de sorgo y pasto varilla crecido en medio Murashige y Skoog (MS) y bajo estrés salino (NaCl 0-400 mM). La aplicación de MWCNT aumentó la tasa de germinación de las semillas de pasto varilla y condujo a una germinación temprana de las semillas de sorgo. Además, observaron que los MWCNT pueden reducir significativamente los síntomas del estrés salino impuestos por la adición de NaCl al medio de crecimiento al mejorar la expresión del gen de las acuaporinas e interactuar con los iones de Na. Joshi et al., (2020) utilizaron MWCNT (70, 80 y 90 $\mu\text{g ml}^{-1}$) para cebar semillas de arroz. Como resultado se observó que las plantas tratadas con MWCNT tenían estomas más densos y raíces de mayor longitud, lo que resultó en un crecimiento más rápido y facilitó la absorción de agua y minerales, aumentando así el rendimiento del cultivo. Además, se mejoró el contenido de clorofila y la actividad fotosintética. Adeel et al., (2021) asperjaron durante 21 días MWCNT (100, 200 y 500 mg L^{-1}) en plantas de *Nicotiana benthamiana* L., posteriormente inocularon con el virus del mosaico del tabaco marcado (TMV). Los resultados demostraron que las plantas tratadas con MWCNT (200 mg L^{-1}) mostraron un fenotipo normal y la sintomatología viral no fue evidente a los 5 días después de la infección. También se demostró que la estructura de los cloroplastos y la fotosíntesis no se vio afectada por la infección por TMV en las plantas tratadas con MWCNT (200 mg L^{-1}) ya que fue igual que las plantas sanas. Además, se indujo al aumento de las fitohormonas relacionadas con las defensas ácido abscísico y ácido salicílico en un 33-52% con la adición de los MWCNT.

Las propiedades superficiales de los CNT (e.g., Grupos funcionales) pueden influir de manera crítica en la respuesta fisiológica de las plantas y a su vez diferentes especies de plantas pueden responder de manera diferente a los CNT en función de sus procesos fisiológicos y la funcionalización de los CNT (Kanth et al., 2020). En este sentido, Pandey et al., (2019) evaluaron MWCNT-COOH (50 y 200 $\mu\text{g ml}^{-1}$) en algodón (*Gossypium hirsutum* L.) y vinca (*Catharanthus roseus* L.). La exposición de las semillas a los NMs

provocó la activación de la germinación temprana de las semillas en *Catharanthus* y una mayor germinación en las semillas de algodón y *Catharanthus*. Se observó un mayor crecimiento de raíces y brotes de plántulas jóvenes de ambas especies probadas. Gohari et al. (2020) evaluaron MWCNTs funcionalizados con COOH (MWCNTs-COOH) (0, 25, 50 y 100 mg L⁻¹) en plántulas de albahaca dulce (*Ocimum basilicum* L.) bajo estrés salino (0, 50 y 100 mM NaCl). Los resultados demostraron que la aplicación de MWCNTs-COOH a una concentración óptima (50 mg L⁻¹) puede mejorar los efectos negativos del estrés por salinidad aumentando el contenido de clorofila y carotenoides e induciendo componentes antioxidantes enzimáticos como la APX, CAT y guayacol peroxidasa y no enzimáticos como los fenoles.

- **Grafeno**

El grafeno es “un cristal bidimensional compuesto por monocapas de átomos de carbono dispuestos en una red en forma de panal con anillos de seis miembros” y es el primer material 2D disponible (Shoala, 2020). Los NMs basados en grafeno (GNMs) tienen muchas propiedades únicas y extraordinarias, como conductividades eléctricas y térmicas superiores y una gran superficie, que los distingue claramente del grafito y los nanotubos de carbono (Sundramoorthy et al., 2018). Los GNMs incluyen el grafeno (prístino), óxido de grafeno (GO), óxido de grafeno reducido (rGO), grafeno de pocas capas (FLG) y puntos cuánticos de grafeno (GQD) y nanohojas de grafeno (GNS) (Wang et al., 2019a). Diversos estudios han evaluado el efecto de los GNMs en diversos cultivos agrícolas de interés comestible e industrial. Los resultados han demostrado efectos positivos que van desde el mejoramiento en la germinación de semillas hasta el incremento en la productividad y el rendimiento de los cultivos. Los GNMs pueden actuar como portadores para liberar lentamente el efecto de un fertilizante y mejorar la eficiencia de utilización de los nutrientes, inhibir el crecimiento de patógenos en las plantas, además, pueden mejorar la tolerancia al estrés por metales pesados, promover el crecimiento de las plantas y mejorar la calidad nutricional (Gao et al., 2020). En general, los GNMs producen respuestas morfológicas, fisiológicas y bioquímicas que ayudan a la planta a tolerar algún estrés ya sea de tipo biótico o abiótico al generar cambios en el transcriptoma, proteoma, metaboloma e ionoma (Youssef et al., 2020).

De igual manera se ha reportado que la aplicación de los GNMs causan toxicidad en las plantas, así mismo, el uso de los GNMs genera preocupaciones sobre un posible impacto negativo en los ecosistemas (Zanelli et al., 2020). No obstante, también se ha demostrado que la concentración adecuada de grafeno puede promover el crecimiento de las plantas, mientras que una alta concentración lo inhibe significativamente. Por tanto, los efectos del grafeno sobre el crecimiento de las plantas están estrechamente relacionados con su concentración y tiempo de tratamiento, así como con el tipo de planta (Song et al., 2020). Chen et al., (2020) evaluaron el mecanismo molecular del grafeno en el crecimiento y desarrollo de maíz (*Zea mays* L.) Las raíces de las plántulas de maíz fueron expuestas a diferentes concentraciones. (0 -100 mg L⁻¹) de grafeno. Los resultados reportaron que la longitud total de las raíces, el volumen de las raíces, el número de ápices y horquillas de las raíces de las plántulas de maíz, al igual que el contenido de nitrógeno y potasio en el suelo alrededor de las raíces fueron favorecidos con adición del grafeno (50 mg L⁻¹). Además, el estudio del transcriptoma mostró expresiones de regulación positiva significativas, las cuales podrían estar relacionadas con los mecanismos subyacentes a la respuesta al grafeno.

Pandey et al., (2019) estudiaron los efectos biológicos del grafeno (0-1000 µg ml⁻¹) en especies productoras de fibra (algodón, *Gossypium hirsutum* L.) y especies ornamentales (vinca, *Catharanthus roseus* L.). La exposición de las semillas al grafeno provocó la activación de la germinación temprana de las semillas de algodón y *Catharanthus*. También se obtuvo un mayor crecimiento de raíces y brotes de plántulas jóvenes de ambas especies. Además, en las plantas de *Catharanthus* suplementadas con grafeno se aceleró la producción total de flores. En el mismo estudio, los cultivos fueron sometidos a estrés salino (50 y 100 mM) y estrés por sequía. Los resultados reportaron mejoras en los rasgos fenotípicos deseados de *Catharanthus* (mayor número de flores y número de hojas) y algodón (mayor biomasa de fibra) al someter las plantas a estrés salino y en condiciones de sequía la adición de grafeno en *Catharanthus* aumentó la supervivencia de la planta sin síntomas de marchitamiento de las hojas. Los autores concluyen que el grafeno no solo mejora la productividad de las plantas en condiciones normales de cultivo, sino que también pueden revertir ciertos síntomas de toxicidad causados por el estrés abiótico.

ARTÍCULO 1

**Seed Priming with Carbon Nanomaterials to Modify the Germination, Growth,
and Antioxidant Status of Tomato Seedlings**



Seed Priming with Carbon Nanomaterials to Modify the Germination, Growth, and Antioxidant Status of Tomato Seedlings

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Abstract: The objective of this work was to determine the responses of tomato seed priming with CNMs (carbon nanomaterials), evaluating the changes in germination and biochemical compounds as well as the effect on the growth of tomato seedlings. Five concentrations of CNMs (10, 100, 250, 500, and 1000 mg L⁻¹) were evaluated, as well as an absolute control and a sonicated control. The results showed that seed priming with CNMs did not affect the germination rate of the tomato seeds; however, it negatively affected the vigor variables, such as the root length (up to 39.2%) and hypocotyl biomass (up to 33%). In contrast, the root biomass was increased by the application of both carbon nanotubes and graphene up to 127% in the best case. Seed priming with carbon nanotubes (1000 mg L⁻¹) decreased the plant height (29%), stem diameter (20%), fresh shoot biomass (63%), fresh root biomass (63%), and dry shoot biomass (71%). Seed priming with graphene increased the content of chlorophylls (up to 111%), vitamin C (up to 78%), β-carotene (up to 11 fold), phenols (up to 85%), and flavonoids (up to 45%), as well as the H₂O₂ content (up to 215%). Carbon nanotubes (CNTs) increased the enzymatic activity (phenylalanine ammonia lyase (PAL), ascorbate peroxidase (APX), glutathione peroxidase (GPX), superoxide dismutase (SOD), and catalase (CAT)). In addition, seed priming with high concentrations of CNMs showed negative effects. Seed

priming with carbon nanomaterials can potentially improve the development of the tomato crop; therefore, this technique can be used to induce biostimulation and provides an easy way to apply carbon nanomaterials.

Keywords: graphene; carbon nanotubes; antioxidants; enzymatic activity; reactive oxygen species

1. Introduction

In recent years, the use of nanotechnology in different areas has increased. Proof of this includes the large number of studies on the application of nanomaterials (NMs), such as metal nanoparticles (NPs) and carbon nanomaterials (CNMs), including single-walled carbon nanotubes (CNTs) (SWCNTs), multi-walled carbon nanotubes (MWCNTs), graphene (GR), and fullerenes [1]. CNMs are of great interest due to their unique chemical and physical properties that make them available for a variety of applications compared to those of the same bulk material [2–4]. Among their main properties are their high rigidity, strength, and elasticity compared to other fibrous materials. In addition, they show a high thermal and electrical conductivity compared to other conductive materials [5]. The literature has reported that nanomaterials (NMs) have the ability to induce biostimulation in plants, generating multiple positive responses, such as increased growth and development, performance, and the ability to tolerate different types of stress [2,4,6,7].

Graphene is a crystalline structure of 2D atomic plane graphite (2D) similar to a honeycomb network and is a basic component for other CNMs; a single layer of graphene rolled into a cylinder forms a SWCNT, while a MWCNT consists of two or more sheets of graphene [8]. These have been shown to be toxic to a variety of species, including vertebrates, algae, bacteria, and fungi [9]. Begum et al. [10] reported that the exposure of cabbage (*Brassica oleracea* var. capitata), tomato (*Lycopersicon esculentum*), and red spinach (*Amaranthus tricolor* and *Amaranthus lividus*) plants to graphene resulted in the inhibition of growth and biomass; in addition, reactive oxygen species (ROS) production and cell death were increased in a concentration-dependent manner. However, Sayes et al. [11] mentioned that the functionalization of the CNMs diminished toxic effects, which could be an alternative solution for this problem.

Favorable effects have also been reported. Zhang et al. [12] showed that the application of graphene oxide (GO) ($40 \mu\text{g mL}^{-1}$) increased the germination of tomato seeds, because the GO penetrated the husks of the seeds, which facilitated the capture of water. In addition, the content of reduced glutathione was increased, as was the activity of the enzymes glutathione reductase, glutathione peroxidase, and glutathione sulfotransferase. In the seedlings of forest species, such as *Larix olgensis*, the application of graphene in low concentrations ($25\text{--}50 \text{ mg L}^{-1}$) was shown to increase the dry matter of

the root, stem and leaves, root length, surface area, volume, and average diameter; however concentrations greater than 100 mg L^{-1} induced the opposite effect [13]. This clearly indicated that the concentration used is decisive in the observed effects regardless of the species in question.

Regarding CNTs, studies have demonstrated that they can penetrate the roots of the plants and then translocate to the vascular bundles and then to the aerial part by means of the xylem through the transpiration process [7]. They can also penetrate the cell wall, as well as its membrane through pores or channels through the apoplastic route and via endocytosis, so that they can be used as carriers of substances or chemicals inside cells [2,14]. However, CNTs can also act as carriers of pollutants, transporting them to the aerial part of the plants [15]. In addition, derived from these characteristics, CNTs can improve the germination of seeds and the growth of plants. Yousefi et al. [16] reported that seed priming with MWCNTs improved the seed germination percentage, mean germination time, and root and stem lengths, as well as the fresh and dry weights of the roots and stems of Hopbush (*Dodonaea viscosa* L.) under drought stress. Martínez-Ballesta et al. [17] showed that broccoli plants (*Brassica oleracea* L. var. Italica) treated with MWCNTs significantly increased their growth (32.7%), and under saline stress conditions, a positive effect was also observed. MWCNTs improved the water absorption in seeds through aquaporins and improved the cation exchange in the cell wall matrix, which increased the concentration of nutrients such as Ca and Fe. These minerals can improve germination and can potentially increase plant growth and development, impacting performance [18]. In addition, the interaction of CNTs with proteins and polysaccharides was found to generate a cascade of signaling that resulted in the accumulation of compounds that led to the thickening of the cell wall and subsequent growth [19].

Several investigations have shown that the applications of these CNMs can have beneficial effects on the growth and development of plants, although inhibition and phytotoxicity can also be observed [2–4,7]. This is because they stimulate the production of ROS by interacting with organelles, such as the mitochondria; additionally, in high concentrations, ROS cause an imbalance in the concentration of antioxidant compounds and in the level of oxidative stress of plants, thus causing damage [9,20,21]. However, ROS can also cause positive effects, as they act as signaling agents under stress conditions, triggering cellular responses to produce antioxidant compounds to counteract ROS, which allows the plant to tolerate stress [22–24].

The tomato crop is considered one of the most important horticultural crops in the world; it is a vegetable with some of the highest demand and highest economic value. The trade and production of tomatoes are particularly important in the tropical, subtropical, and temperate regions, both for the markets of fresh products and for processing [25]. It is especially important to look for new alternatives based on nanotechnology that allow for improvements in the operation of agricultural crops and that are easy to apply. Therefore, it is very important to study the impact that CNMs can have on production systems in order to improve them. In this context, the present work was developed with

the objective of determining the responses of the exposure of tomato seeds to different doses and types of CNMs, evaluating the changes in germination and biochemical compounds, as well as the effect on the growth of seedlings in the short term.

2. Materials and Methods

The experiment was developed in two stages, one in the laboratory and one in the greenhouse. In the laboratory stage, a germination test was carried out on tomato seeds, while in the greenhouse stage, the effect of seed priming with carbon nanomaterials on tomato seedlings was evaluated. In both stages, the seeds were treated with the different carbon nanomaterials. “Pony” hybrid tomato seeds (Harris Moran, Davis, CA, USA) of the saladette type with determined growth were used.

2.1. Characteristics of Carbon Nanomaterials

Two types of carbon nanomaterials were used: carbon nanotubes and graphene. The carbon nanotubes (CNTs) were multilayer, with an out diameter of 30–50 nm, a length of 10–20 μm , and a purity of approximately 95% (Nanostructured and Amorphous Materials, Inc., Houston, TX, USA). The graphene (GR) used was multilayer, with a diameter of 2 μm , a thickness of 8–12 nm, and a purity of 97% (Cheap Tubes Inc., Cambridgeport, VT, USA). The dispersion of the CNMs was determined through the Z potential using a Z potential analyzer (ZetaCheck, ZC 0006, Microtrac, Montgomery, PA USA) at -39.1 mV for the CNTs and -35.2 mV for the GR.

2.2. Seed Priming and Description of Treatments

The tomato seeds were sterilized in a 2% (v/v) solution of sodium hypochlorite for 5 min and rinsed five times with distilled water. Five concentrations were evaluated for each of the CNMs: 10, 100, 250, 500, and 1000 mg L^{-1} . The solutions were prepared in 50 mL beakers containing 75 tomato seeds dispersed in 20 mL of solution (distilled water + CNMs). Subsequently, they were directly sonicated in an ultrasonicator (Q500 sonicator, QSONICA, Melville, NY, USA). The sonication amplitude of vibration (60%) was kept constant for 10 min at 20 KHz, similarly to what was reported by Ratnikova et al. [26]. This process is necessary, as carbon-based nanomaterials (CBNMs) tend to agglomerate due to van der Waals forces [27]. To study their applications, the CBNMs must be uniformly dispersed because, in addition to the mass concentration and primary particle size, the level of agglomeration can also play a critical role in determining effects on plants [28]. After sonication, the seeds were stored in jars with lids along with the solution of CNMs for 24 h. To verify that the solution was stable, it was manually shaken every eight hours, thus stopping the CNMs from precipitating. In addition to the treatments, we included an absolute control in which only distilled water was used and no sonication was applied, as well as a sonicated control following the same previously described process.

2.3. Germination Test

We placed 10 tomato seeds on filter paper for each Petri dish (diameter of 125 mm). Each Petri dish was considered as a replicate, and each consisted of four replicates. The Petri dishes were covered and placed randomly in a germination chamber (Plant Growth

Chamber Model 250) at a temperature of 25 ± 1 °C with 16 h of light per day. To maintain the moisture of the seed, distilled water was added when required. After 15 days, the percentage of germination, the length of the root and the hypocotyl, and the fresh biomass of the hypocotyl and the root were determined.

2.4. Greenhouse Experiment

After seed priming with CNMs for 24 h, a seed was placed in a 1 L polystyrene cup (L) with a mix of perlite substrate and peat moss in a 1:1 ratio. We considered a total of 10 cups for each treatment, where each vessel was a repeat. A directed irrigation system was used for irrigation, applying a Steiner solution (1961) at a 25% concentration to provide the necessary nutrients. The pH of the nutrient solution was adjusted with sulfuric acid (98%) to 6.5. The tomato plants were grown for 60 days in a chapel-type greenhouse, with a polycarbonate cover, an average PAR (photosynthetically active radiation) of $600 \mu\text{mol m}^{-2} \text{s}^{-1}$, a temperature of 28 °C, and relative humidity of 60%. Sixty days after planting, the plant height, stem diameter, and number of leaves were measured. In addition, the fresh and dry biomass of the aerial part and the root were determined. For the determination of the biochemical compounds, samples of fresh foliar tissue were taken from fully expanded young leaves (third and fourth leaves), and these were placed in a freezer at -20 °C and then lyophilized for 72 h in freeze dryer (Labconco, FreeZone 2.5 L model, Kansas City, MO, USA). The lyophilized samples were ground to a fine powder to make the determinations.

2.5. Biochemical Determinations

2.5.1. Photosynthetic Pigments

The chlorophyll content was determined according to the method of Nagata and Yamashita [29]. The absorbance at 645 and 663 nm was determined and used in Equations (1) and (2) to determine the content of chlorophyll, as follows:

$$\text{Chl a} = 0.999 \times \text{Abs}_{663} - 0.0989 \times \text{Abs}_{645}, \quad (1)$$

$$\text{Chl b} = -0.328 \times \text{Abs}_{663} + 1.77 \times \text{Abs}_{645}. \quad (2)$$

The total chlorophyll is the sum of Chl a and Chl b. All data are expressed as mg g^{-1} dry weight (mg g^{-1} DW).

2.5.2. Non-Enzymatic Antioxidant Compounds and Antioxidant Capacity

The non-enzymatic antioxidant compounds were determined according to standard techniques.

The Vitamin C (mg g^{-1} DW) content was determined by the colorimetric method using 2,6 dichlorophenol, 1 g of dry tissue, and HCl (2%), as described in Padayatt et al. [30].

The β -carotene content was determined according to the method of Nagata and Yamashita [29]. The absorbance at 453, 505, 645, and 663 nm was determined and used in Equation (3) as follows:

$$\beta^- \text{ carotene} = 0.216 \times \text{Abs}_{663} - 1.22 \times \text{Abs}_{645} - 0.304 \times \text{Abs}_{505} + 0.452 \times \text{Abs}_{453}. \quad (3)$$

The phenols (mg g^{-1} DW) were determined using the Folin–Ciocalteu reagent, as described in [31]. The sample (0.2 g) was extracted with 1 mL of a water:acetone solution (1:1). The mixture was vortexed for 30 s. The tubes were centrifuged (UNICO Spectrophotometer Model UV2150, Dayton, USA) at $17,500 \times g$ for 10 min at 4°C . In a test tube, 50 μL of the supernatant, 200 μL of the Folin–Ciocalteu reagent, 500 μL of 20% sodium carbonate (Na_2CO_3), and 5 mL of distilled water were added and then vortexed for 30 s. The samples were placed in a water bath at 45°C for 30 min. Finally, the reading was taken at an absorbance of 750 nm using a plastic cell in a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, USA).

The flavonoids (mg g^{-1} DW) were determined with the method of Arvouet-Grand et al. [32]. For the extraction, 100 mg of lyophilized tissue was placed in a test tube, where 10 mL of reagent-grade methanol was added and shaken for 30 s until the mixture was homogenized. The mixture was filtered using No. 1 Whatman paper. For the quantification, 2 mL of the extract and 2 mL of methanolic solution of aluminum trichloride (AlCl_3) 2% were added to a test tube and left to rest for 20 min in the dark. The reading was then taken in a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA) at a wavelength of 415 nm using a quartz cell.

The total protein (mg g^{-1} of DW) determination was performed using Bradford's colorimetric technique [33]. In a microplate, 5 μL of the extract and 250 μL of the Bradford reagent were placed in each well. They were incubated for 10 min at room temperature (26°C) and then read at a wavelength of 630 nm on a microplate reader (Allsheng, AMR-100 model, Hangzhou, China).

The glutathione (GSH) content ($\mu\text{mol g}^{-1}$ DW) was determined using the method of Xue et al. [34] by means of a 5,5-dithio-bis-2 nitrobenzoic acid (DTNB) reaction. A mix of 0.480 mL of the extract, 2.2 mL of sodium dibasic phosphate (Na_2HPO_4 at 0.32 M), and 0.32 mL of the DTNB dye (1 mM) was placed in a test tube. Then, the mix was vortexed and read on a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA) at 412 nm using a quartz cell.

The antioxidant capacity was determined using the DPPH (2,2-diphenyl-1-picrylhydrazyl) radical according to the method of Brand-Williams et al. [35]. The hydrophilic compounds were determined using a phosphate buffer for extraction, and for the lipophilic compounds, a hexane:acetone solution was used. The total antioxidant capacity was obtained by the sum of the hydrophilic and lipophilic compounds [36]. The antioxidant capacity was expressed as vitamin C equivalents (mg g^{-1} DW).

2.5.3. Hydrogen Peroxide

The extraction was carried out according to the methodology of Patterson et al. [37]. We ground 50 mg of lyophilized tissue to powder together with 5 mL of 5% trichloroacetic

acid (TCA) and 150 mg of activated charcoal. Subsequently, this mixture was centrifuged at $10,000\times g$ for 20 min at $4\text{ }^{\circ}\text{C}$. From the resulting supernatant, 0.5 mL was taken and passed to a 15 mL conical tube containing 2.5 mL of TCA, to which a 10% ammonia solution was added until a pH of 8.4 was reached. The solution was filtered with a 0.45 micron pore syringe and polytetrafluoroethylene (PTFE) membrane. The filtrate was divided into two aliquots of 1 mL. To one of these aliquots (aliquot blank), we added 8 μg of catalase and maintained the solution at room temperature ($24 \pm 1\text{ }^{\circ}\text{C}$) for 10 min. Subsequently, for both aliquots with and without catalase (sample), 1 mL of the colorimetric reagent was added and allowed to incubate for 10 min at $30\text{ }^{\circ}\text{C}$. After the reaction time, the absorbance at 505 nm was determined by a UV–VIS spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA). The colorimetric reagent was prepared with 10 mg of 4-aminoantipyrine, 10 mg of phenol, and 5 mg of peroxidase (150 U mg^{-1}), which were dissolved in 50 mL of an acetic acid buffer (100 mM, pH 5.6). The content of H_2O_2 was given on a standard curve.

2.5.4. Enzymatic Activity

The extract used was the same as that used for total proteins and followed the standard techniques. The ascorbate peroxidase (EC 1.11.1.11) was determined by the method of Nakano and Asada [38] and is expressed as U per gram of total proteins ($\text{U g}^{-1}\text{ TP}$), where U is equal to the μmol of oxidized ascorbate per milliliter per minute. The measurement was undertaken at two moments (at time 0 (T_0) and at time 1 (T_1)). At T_0 , a mix of 100 μL of extract, 500 μL of ascorbate (10 mg L^{-1}), 400 μL of H_2SO_4 (5%), and 1 mL of H_2O_2 (100 mM) were placed in a test tube and then vortexed for 30 s. The absorbance was measured in a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA) at 266 nm with a quartz cell. At T_1 , 100 μL of extract, 500 μL of ascorbate (10 mg L^{-1}), and 1 mL of H_2O_2 (100 mM) were added to the previous mixture and vortexed for 1 min at a temperature of $26\text{ }^{\circ}\text{C}$. To stop the reaction, 400 μL of H_2SO_4 (5%) was added, and the absorbance was measured. Ascorbate peroxidase determination was based on the quantification of the ascorbate oxidation rate by means of the absorbance difference (T_0-T_1).

The glutathione peroxidase (EC 1.11.1.9) ($\text{U per gram of total proteins (U TP}^{-1}$), where U is equal to the mM equivalent of reduced glutathione (GSH) per milliliter per minute) was determined by the method of Flohé and Günzler [34,39]. A mix of 200 μL of extract, 400 μL of GSH (0.1 mM), and 200 μL of Na_2HPO_4 (0.067 M) was placed in a test tube. The mixture was preheated in a water bath at $25\text{ }^{\circ}\text{C}$ for 5 min, and then 200 μL of H_2O_2 (1.3 mM) was added to start the catalytic reaction for 10 min at a temperature of $26\text{ }^{\circ}\text{C}$. The reaction was stopped by the addition of 1 mL of 1% trichloroacetic acid. The mixture was placed in an ice bath for 30 min and then centrifuged at $1008\times g$ for 10 min at $4\text{ }^{\circ}\text{C}$. To assess the glutathione peroxidase, 480 μL of the supernatant, 2.2 mL of Na_2HPO_4 (0.32 M), and 320 μL of 1 mM DTNB were placed in a test tube. The absorbance was measured by a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA) at 412 nm with a quartz cell.

The catalase (EC 1.11.1.6) ($U\ TP^{-1}$, where U is equal to the mM equivalent of H_2O_2 consumed per milliliter per minute) was quantified by the method of Dhindsa et al. [40]. The measurement was carried out in two steps (at time 0 (T0) and at time 1 (T1)). At T0, 100 μ L of extract, 400 μ L of H_2SO_4 (5%), and 1 mL of H_2O_2 (100 mM) were added to an Eppendorf tube and vortexed for 30 s. The absorbance was then measured on a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA) with a quartz cell at 270 nm. At T1, 100 μ L of extract and 1 mL of H_2O_2 (100 μ L) were added and stirred for 1 min in a vortex at 26 °C. Then, 400 μ L of H_2SO_4 (5%) was added to stop the reaction, and the absorbance was measured by a UV–Vis spectrophotometer with a quartz cell at 270 nm. The determination of catalase was based on the quantification of the oxidation rate of H_2O_2 by absorbance difference (T0–T1).

The phenylalanine ammonia lyase (PAL) (EC 4.3.1.5) was determined according to the method of Sykłowska-Baranek et al. [41], and the results are expressed as U per gram of total proteins ($U\ g^{-1}\ TP$), where U is equal to μ mol equivalent of trans-cinnamic acid per milliliter per minute. A total of 0.1 mL of the enzymatic extract was taken, and 0.9 mL of L-phenylalanine (6 mM) was added. After 30 min of incubation at 40 °C, the reaction was stopped with 0.25 mL of 5 N HCl. The samples were placed in an ice bath, and 5 mL of distilled water was added. The absorbance was determined at 290 nm on a UV–Vis spectrophotometer (UNICO Spectrophotometer Model UV2150, Dayton, NJ, USA).

The superoxide dismutase (SOD) (EC 1.15.1.1) ($U\ mL^{-1}$, where U is defined as the amount of enzyme needed to exhibit 50% dismutation of the superoxide radical) was carried out using the Cayman kit (SOD Assay Kit 706002, Cayman Chemical, Ann Arbor, Michigan, USA). A mix of 20 μ L of extract, 200 μ L of the radical detector (tetrazolium salt), and 20 μ L of xanthine oxidase solution was placed in a microplate. The microplate was covered with a transparent cover (kit), stirred for 10 s, and then incubated at 26 °C for 30 min. The absorbance was then measured at a length of 450 nm using a plate reader (Allsheng, AMR-100 model, Hangzhou, China). The principle of the test was based on the use of a tetrazolium salt for the detection of superoxide radicals generated by xanthine oxidase and hypoxanthine.

2.6. Statistical Analysis

For the germination test, four replicates were used per treatment. The variables of tomato growth were assessed using 10 replicates, where a plant was used a replicate. For each of the evaluated biochemical variables, five replicates per treatment were used. A completely random design was used. An analysis of variance and Fisher's least significant difference (LSD) mean test ($p < 0.05$) were performed. A Pearson correlation analysis was also performed between the different evaluated antioxidants. All statistical procedures were performed using the software Infostat 2018 (<http://www.infostat.com.ar>).

3. Results and Discussion

3.1. Germination Test

For the germination variables, only the length of the hypocotyl was unaffected with any concentration of the CNMs applied, while for the rest of the variables, we observed differences between the treatments (Figure 1). The percentage of germination was affected by the application of GR at its highest dose (1000 mg L^{-1}), presenting 19% less germination compared to the absolute control, and the rest of the treatments with CNMs were equal to this (Figure 1A). The root length decreased with the application of 500 mg L^{-1} of GR and 10 mg L^{-1} of CNTs compared to the absolute control by 37.2% and 39.2%, respectively (Figure 1B). The addition of GR decreased the hypocotyl biomass by 30.11%, 33.05%, and 32%, with the doses of 250, 500, and 1000 mg L^{-1} , respectively, while 250 mg L^{-1} of CNTs presented a decrease of 30.94% in relation to the absolute control (Figure 1E). In contrast, the root biomass increased by 66% and 127.2% with the application of 100 mg L^{-1} of GR and CNTs, respectively, compared to both controls (sonicated and non-sonicated); the rest of the treatment results were the same (Figure 1D).

The results indicated obtained, in general, that CNMs could negatively affect some variables related to germination in a concentration-dependent manner, mainly high concentrations of GR. However, we observed that root development could be increased with the application of CNMs.

Pandey et al. [42], evaluated graphene and MWCNTs at concentrations of 50 and 200 mg L^{-1} in sorghum and millet seeds incubated for 10 and 21 days in an MS (Murashige and Skoog) culture medium. They observed an increase in the percentage of germination, as well as a more rapid germination of both seeds. They also mentioned that the concentration of 50 mg L^{-1} for both nanomaterials was more effective because it increased the length of the shoots and roots, as well as the fresh biomass.

Khodakovskaya et al. [14] reported that the germination of seeds and the development of tomato seedlings drastically improved after exposure to 40 mg L^{-1} of CNTs in an MS culture medium, after evaluation for 21 days. According to the authors, the observed results were due to the penetration of the CNTs through the cover of the seed by creating a greater number of pores, which allowed for a greater uptake of water in the seeds. Khodakovskaya [43] mentioned that CNTs ($50, 100$ to 200 mg L^{-1}) applied in tomatoes in an MS medium activated many genes related to stress, among which the protein gene of the water channel stood out. This resulted in the better germination and growth of the tomato seedlings. Begum et al. [10] reported that high concentrations of graphene (2000 mg L^{-1}) inhibited the growth of the tomato roots and shoots, in addition to decreasing the biomass. However, graphene concentrations of 50 – 200 mg L^{-1} did not affect the tomato plant [43]. Several authors have mentioned that the phytotoxicity of CNMs depends on the type of seed, species of plant, the stage of growth of the plant, the nature of the CNMs, and the dose and exposure time [4,7,44,45]. However, in general and according to the results obtained in this work, it is clear that high doses of CNMs are more likely to induce negative responses in the germination of tomato seeds.

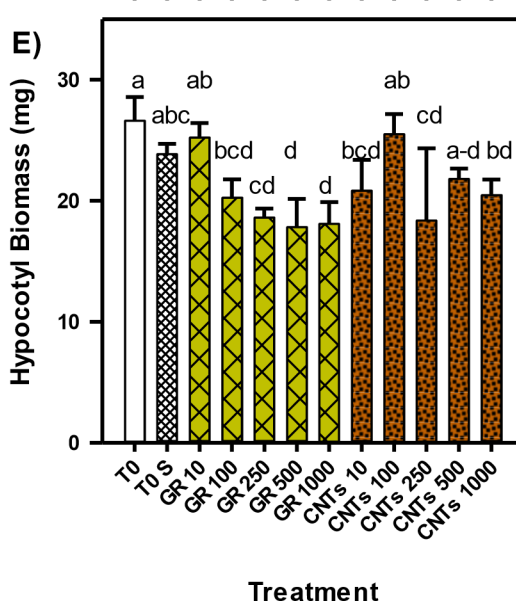
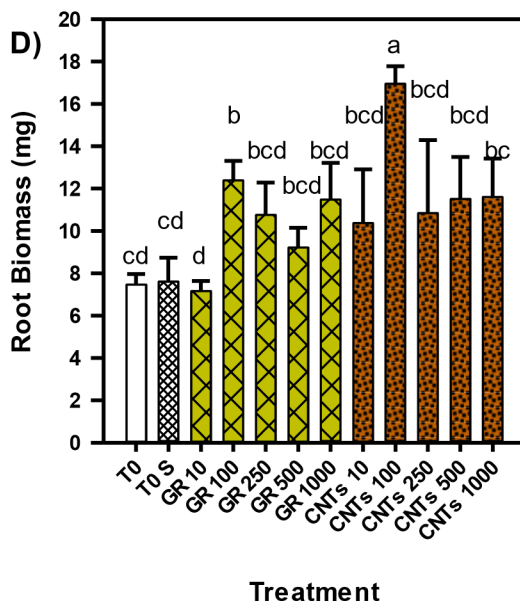
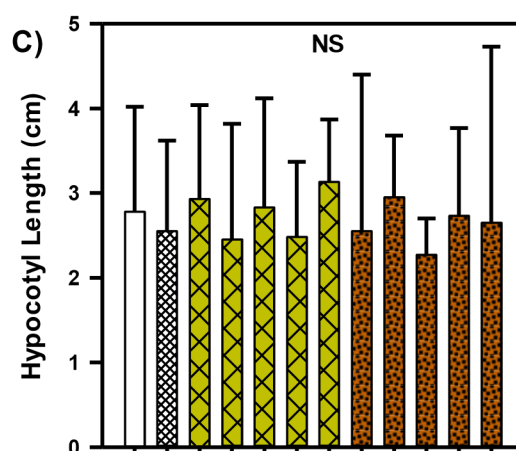
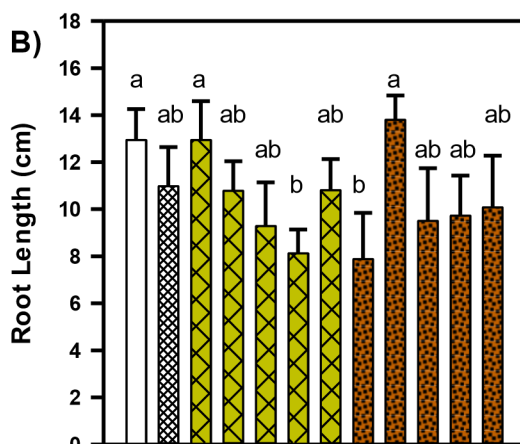
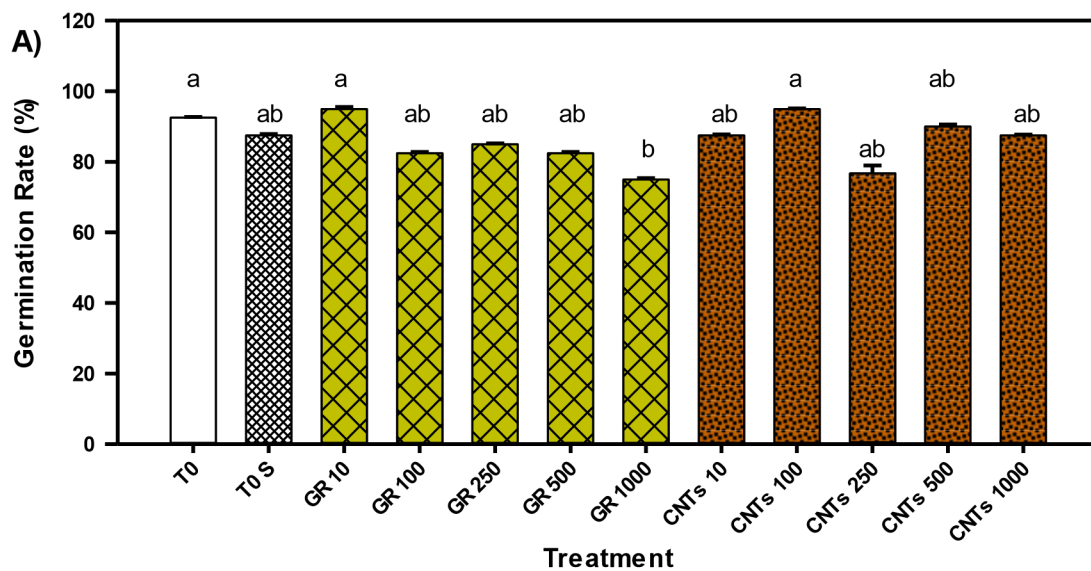


Figure 1. Germination variables evaluated in tomato seeds treated with carbon nanomaterials. Each data point is the average of four replicates \pm standard error. Different letters indicate significant differences between treatments according to Fisher's least significant difference test ($p \leq 0.05$). T0: absolute control. T0 S: sonicated control. GR: graphene. CNTs: carbon nanotubes.

3.2. Impact of Seed Priming on Growth of Tomato Seedlings

The agronomic variables evaluated in the tomato plants treated with the CNMs showed significant differences between treatments (Figure 2). In general, the results showed that the process of the sonication of the seeds affected the behavior of the agronomic variables, since in all cases, the sonicated control presented the lowest values of the evaluated variables. On the other hand, the absolute control was lower than some treatments with CNMs only in root dry biomass, and it was the best in dry shoot biomass. Meanwhile, in the rest of the evaluated variables, it was the same as the best treatment with CNMs.

In comparison to the sonicated control, the evaluated variables behaved in the following way. The plant height increased by 41.75% and 41.25% with the addition of GR and CNTs, respectively, with the dose of 10 mg L^{-1} (Figure 2A). The stem diameter increased with the GR 10 and 250 treatments by 13.24% and 11.58%, respectively (Figure 2B). The fresh shoot biomass increased by 49.52% with GR and 45.05% with CNTs, both with a dose of 10 mg L^{-1} (Figure 2C). The fresh root weight increased by 40.37% with the addition of GR 1000 compared with the sonicated control, contrary to that observed with CNTs 1000, which decreased by 47.32% (Figure 2D). The dry shoot biomass increased by 42.70% with GR and 41.08% with CNTs, both with a dose of 10 mg L^{-1} (Figure 2E), while the dry root biomass was increased in the GR 1000 treatment by 197.5% (Figure 2F).

Compared to the absolute control, the results were different when derived from the process of sonicating the seeds. The dry root biomass was better with the GR 1000 treatment with an increase of 112% (Figure 2F). On the other hand, the plant height was lower with concentrations of 100, 500, and 1000 mg L^{-1} of CNTs by 9.8%, 9.6%, and 29%, respectively (Figure 2A). The stem diameter decreased with all evaluated doses of CNTs (Figure 2B), and the dry shoot biomass also decreased with all treatments that included CNMs (Figure 2E). In general, the obtained results showed that high doses of CNMs ($500\text{--}1000 \text{ mg L}^{-1}$) generated adverse effects in the evaluated variables, although we observed that the CNTs had more effects than the GR (Figure 2).

In relation to the process of the sonication of the seeds, Ratnikova et al. [26] mentioned that there was a mechanical effect that removes a part of the seed coat that improved the water uptake and accelerated the appearance of the radicle. They also proposed that the removal or rupture of this layer channels allowed for the passage of small molecules to the embryo, which could improve the penetration of the CNMs to increase the results observed in the treatments with CNMs compared to the sonicated control.

Pandey et al. [42] reported an increase in fresh biomass (28.11%) and dry biomass (16.66%) of sorghum and millet plants treated with graphene (50 and 200 mg L⁻¹) that was applied via soil under greenhouse conditions. In seedlings of *Larix olgensis*, low concentrations of graphene (25–50 mg L⁻¹) increased the dry matter of the root, stem and leaves, root length, surface area, volume, and average diameter; in contrast, concentrations greater than 100 mg L⁻¹ induced the opposite effect [13]. Similarly, Villagarcia et al. [18] showed that the CNTs (40 mg L⁻¹) in an MS culture medium increased their absorption of water and that the addition of calcium and iron improved the growth and development of tomato plants.

Yousefi et al. [16] reported that seed priming with MWCNTs improved the seed germination percentage, mean germination time, and root and stem lengths, as well as the fresh and dry weights of the roots and stems of Hopbush (*Dodonaea viscosa* L.) under drought stress. Martínez-Ballesta et al. [17] showed that broccoli plants (*Brassica oleracea* L. var. *Italica*) treated with MWCNTs significantly increased their growth under saline stress conditions. Liu et al. [46] mentioned that CNTs had physicochemical properties as molecular transporters in the cell walls of plants, which stimulated the growth of crops and promoted the metabolism of crop growth. This indicated that the concentration used was decisive in the effects observed, though the species may be more or less tolerant to CNMs, which could have also defined the observed response.

On the other hand, studies have demonstrated that, when entering cells, especially in the roots, CNTs form aggregates that could cause negative effects by obstructing the transport of nutrients and, in turn, causing a delay in growth [9,46,47]. In addition, CNTs have been found to generate reactive oxygen species and, consequently, oxidative stress that modify the physiological and biochemical responses of plants exposed to these CNMs [48]. This explains the negative effects observed here with high doses of CNMs.

3.3. Content of Photosynthetic Pigments of Tomato Seedlings

The chlorophyll a, b, and total contents were consistently increased with the addition of graphene in all the studied doses (Figure 3). The addition of GR (10–1000 mg L⁻¹) increased chlorophyll a, with the dose of 100 mg L⁻¹ being the one that generated the best result with increments of 120% and 99% in comparison with the absolute and sonicated controls, respectively (Figure 3A). Chlorophyll b also increased with the application of GR, where the low concentrations (10, 100, and 250) obtained the highest chlorophyll b content in the ranges of 82%–100% and 56%–71% compared to the absolute and sonicated controls, respectively (Figure 3B). In the total chlorophyll content, the GR 100 treatment generated an increase of 111% compared to the absolute control and 87.53% compared to the sonicated control (Figure 3C). As for CNTs, the addition of 500 and 1000 mg L⁻¹ increased the chlorophyll a content by 41.6% and 43%, respectively (Figure 3A), and only the 1000 mg L⁻¹ dose increased the total chlorophyll by 40.9% compared to the absolute control (Figure 3C). Chlorophyll b was not affected by the addition of CNTs (Figure 3B).

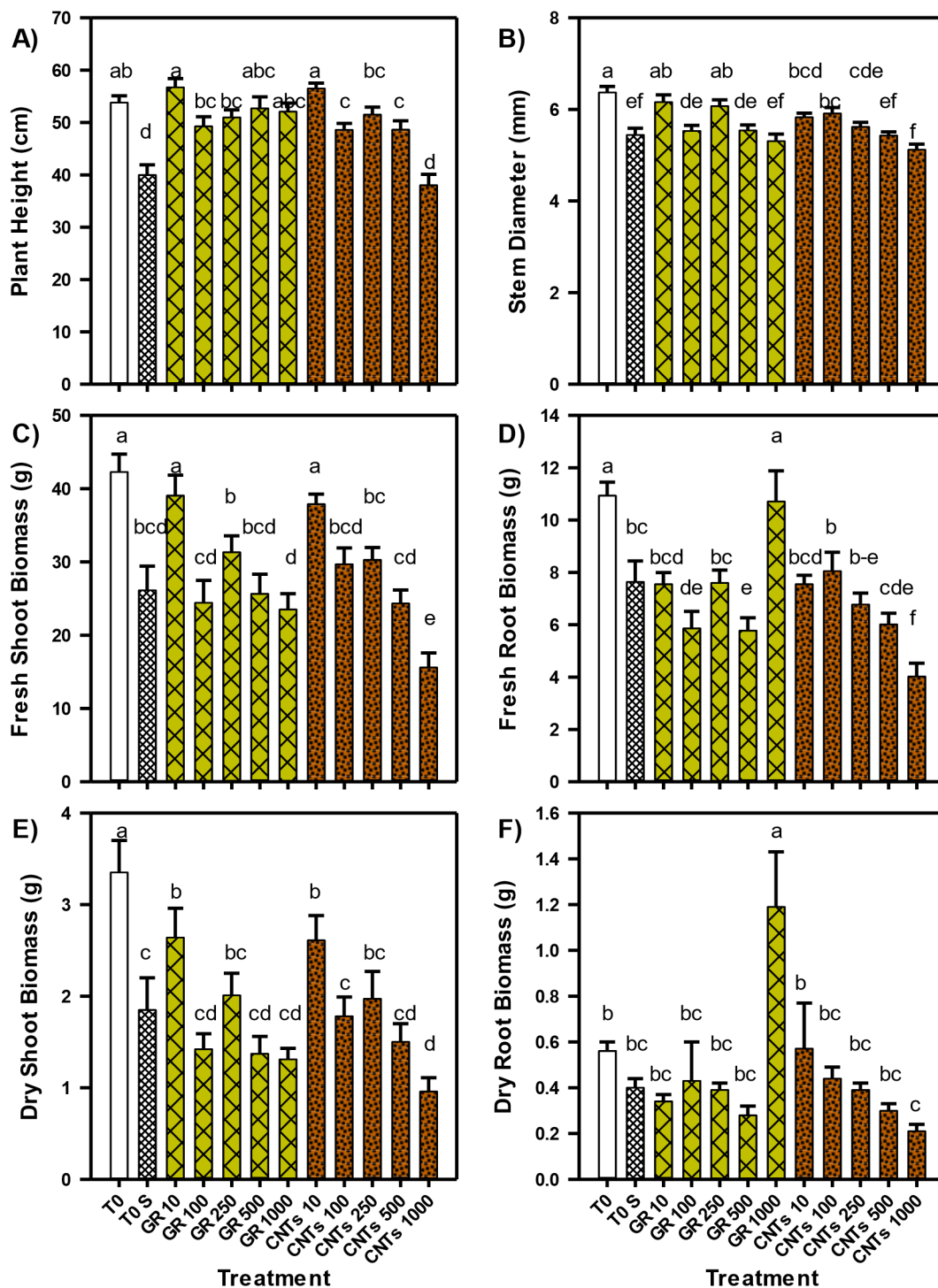
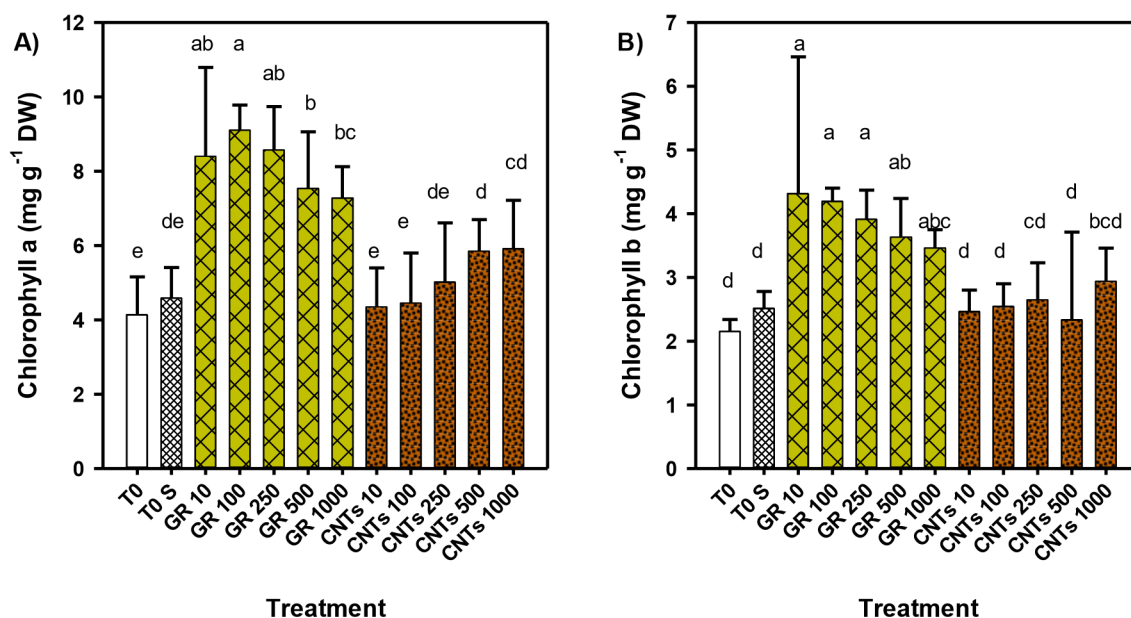


Figure 2. Agronomic variables evaluated in tomato seedlings treated with carbon nanomaterials. Each data point is the average of ten replicates \pm standard error. Different letters indicate significant differences between treatments according to Fisher's least significant difference test ($p \leq 0.05$). T0: absolute control. T0 S: sonicated control. GR: graphene. CNTs: carbon nanotubes.

An increase of the chlorophyll in plants modifies the absorption of light and therefore the production of carbohydrates, making the process more efficient. Wang et al. [49] reported that the application of carbon dots (0.02–0.12 mg mL⁻¹) in mung bean shoots increased the chlorophyll content (14.8%). Park and Ahn [50] evaluated the effect of CNTs (500 mg L⁻¹) on the content of chlorophyll in carrot leaves suspended for 48 h in a solution and reported an increase of 25%–30%. Giraldo et al. [51] mentioned that CNTs have the potential to move from the soil to the plants and to be located within the cells of the leaves, especially within chloroplasts, and thus promote photosynthetic activity, because this modifies the activity of the chloroplast in carbon capture through the promotion of energy use and electron transport rates. Larue et al. [52] reported that the application of CNTs (50 mg L⁻¹) in wheat seedlings did not affect the photosynthetic activity, as the chlorophyll a and b contents remained unchanged.

With respect to graphene, Zhang et al. [53] evaluated different doses (250, 500, 1000, and 1500 mg L⁻¹) in the roots and shoots of wheat plants after 30 days of exposure, and as a result, the chlorophyll content and PSII (photosystem II) activity were reduced. Siddiqui et al. [54] evaluated the effect of graphene oxide (0.05 and 0.10 mg mL⁻¹) sprinkled on carrot leaves and reported a decrease in chlorophyll content.

The mentioned results showed that both positive and negative effects could be observed with the application of CNMs, though it was clear that this depended on the route of application, dose, type of material, and exposure times. The results obtained in this study showed that the graphene application was more efficient than that of the CNTs in increasing the chlorophyll content, at least until the time of sampling (60 days after planting). In addition, no nanotoxicity was observed with any dose of the CNMs evaluated, as there was no decrease in chlorophylls until the moment of analysis.



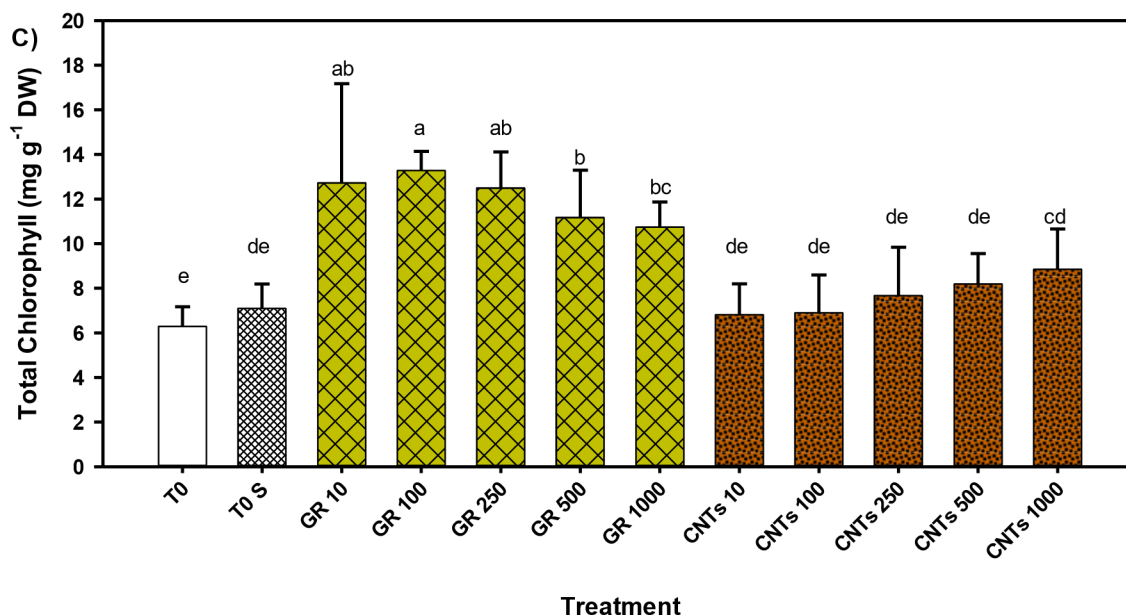


Figure 3. The contents of chlorophylls in the leaves of tomato seedlings treated with carbon nanomaterials. Each data point is the average of five replicates \pm standard error. Different letters indicate significant differences between treatments according to Fisher's least significant difference test ($p \leq 0.05$). T0: absolute control. T0 S: sonicated control. GR: graphene. CNTs: carbon nanotubes. DW: dry weight.

3.4. Antioxidant Status of Tomato Seedlings

The obtained results showed that for the proteins, vitamin C, β -carotene, phenols, flavonoids, the antioxidant capacity of lipophilic compounds, and the total antioxidant capacity, at least one treatment was better than the absolute control (Figures 4 and 5). Only in the content of GSH and the antioxidant capacity of hydrophilic compounds was there no treatment greater than the absolute control (Figure 4B). Regarding H_2O_2 production, the GR 500 and 1000 treatments together with the absolute control presented the lowest H_2O_2 values, while the GR 100 and 10 treatments presented the highest values at around 2.5 times more than the absolute control (Figure 4F).

The GR 1000 treatment generated the highest concentration of vitamin C (Figure 4A), H_2O_2 (Figure 4F), and phenols (Figure 4C), which were 18.4%, 78%, and 85.2% more than the absolute control, respectively. The β -carotene content was better with the GR 250 treatment (10 times more than the absolute control) (Figure 4E), while the GR 100 treatment generated the highest flavonoid content (45.4% more than the absolute control) (Figure 4D); in both cases, the GR 1000 treatment was also better than the absolute control by nine-fold and 43.3%, respectively. These results inversely corresponded with the H_2O_2 because the highest doses of graphene (500 and 1000 mg L^{-1}), together with the absolute control, induced the lowest accumulation of this radical, which was expected as one of the functions of the antioxidant compounds is to neutralize the ROS. However, graphene at 100 mg L^{-1} increased the H_2O_2 up to 215%, and at 10 mg L^{-1} , graphene increased it by 195% (Figure 4F).

Regarding antioxidant capacity, the CNTs 250 treatment induced the best results in the antioxidant capacity of lipophilic compounds that were greater than the absolute control by 23.2% (Figure 5B); meanwhile, the total antioxidant capacity was higher by 19.5% (Figure 5C). In contrast, all graphene treatments showed significantly lower values than the absolute control in these variables (Figure 5).

It is well known that non-enzymatic antioxidant compounds, such as vitamin C, glutathione, and carotenoids, play a fundamental role in the control of ROS. Vitamin C is a powerful antioxidant that protects plants from oxidative damage by acting as a substrate in reactions catalyzed by the enzyme ascorbate peroxidase (APX) by reducing H_2O_2 to H_2O [55]. Vitamin C also plays an important role in photosynthesis as a cofactor of enzymes (including the synthesis of ethylene, gibberellins, flavonoids, and anthocyanins) [56]. Carotenoids are lipophilic compounds that act as non-enzymatic antioxidant compounds by preventing the formation or elimination of $^1\text{O}_2$ by the xanthophyll cycle, and they function as antenna molecules, capturing light in chloroplasts [57,58].

The main role of β -carotene in green tissues is the extinction of $^3\text{Chl}^*$, thus providing the inhibition of the production and damage of $^1\text{O}_2$, in addition to participating in the formation of provitamin A [59]. Glutathione is one of the most important antioxidants that detoxifies ROS and protects plants from oxidative damage by eliminating H_2O_2 , $^1\text{O}_2$, OH^\bullet , and $\text{O}_2^{\bullet-}$ [60]; it also participates in the regeneration of ascorbic acid [61]. Phenolic compounds also have the ability to eliminate free radicals due to their role as electron donors and their ability to chelate transition metal ions and terminate the Fenton reaction [62].

Among these compounds, for example, the flavonoids found in the chloroplast act as singlet oxygen scavengers and chloroplast membrane stabilizers by altering the kinetics of peroxidation and decreasing the fluidity of the membranes [63]. These changes could seriously hinder the diffusion of ROS and restrict peroxidative reactions [59]. Thus, an increase in this compound could generate a secondary pathway to eliminate ROS and improve the antioxidant defense system [64]. Therefore, an increase in this type of compounds in plants may lead to a greater capacity to tolerate oxidative stress caused, in turn, by other types of stress.

According to the results obtained in this study, it was clear that the application of CNMs induced the production of non-enzymatic antioxidant compounds, as also shown by Siddiqui et al. [54] who reported increases in the carotenoid content in carrot crops by the foliar application of graphene oxide (0.05–0.10 mg mL^{-1}). Begum and Fugetsu [44] demonstrated that ascorbic acid decreased oxidative stress caused by CNTs (0–1000 mg L^{-1}) in red spinach developed under hydroponic conditions.

The increase in the content of antioxidant compounds observed was due to the fact that CNMs stimulate ROS production by interacting with cell organelles [65]. H_2O_2 , which is one of the main ROS, has a double function. In low concentrations, it acts as a signaling agent, activating the production of antioxidant compounds; however, in excess,

it generates oxidative stress [22–24]. Anjum et al. [66] showed that doses of 100, 200, and 1600 mg L⁻¹ of graphene oxide impaired the metabolism of glutathione due to the greater accumulation of ROS in *Vicia faba*. However, moderate concentrations of this same CNM (400 and 800 mg L⁻¹) generated different effects and, on the other hand, increased the glutathione content while decreasing the ROS [67].

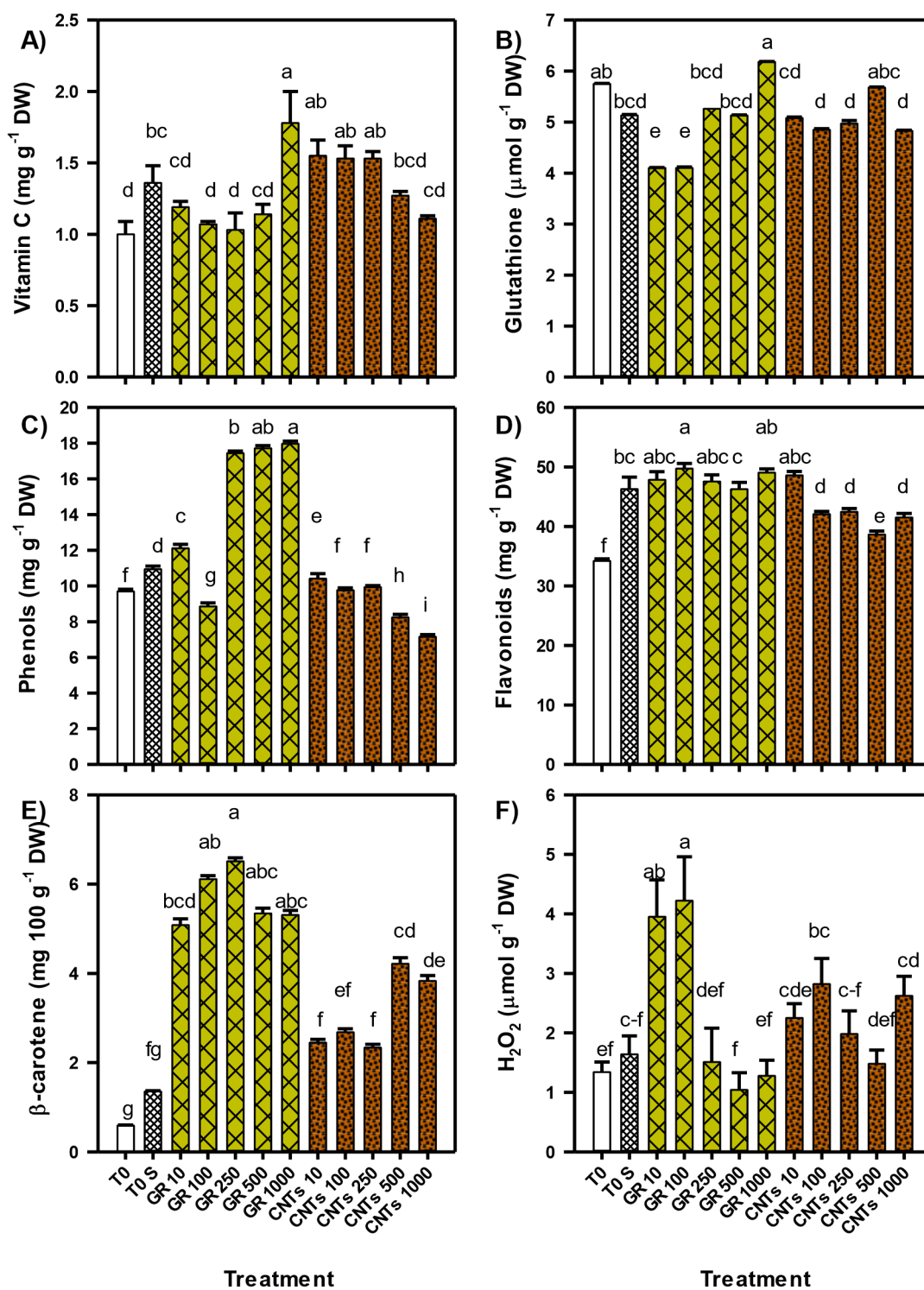


Figure 4. Antioxidant compounds and hydrogen peroxide (H_2O_2) in the leaves of tomato seedlings treated with carbon nanomaterials. Each data point is the average of five replicates \pm standard error. Different letters indicate significant differences between treatments according to Fisher's least significant difference test ($p \leq 0.05$). T0: absolute control. T0 S: sonicated control. GR: graphene. CNTs: carbon nanotubes. DW: dry weight.

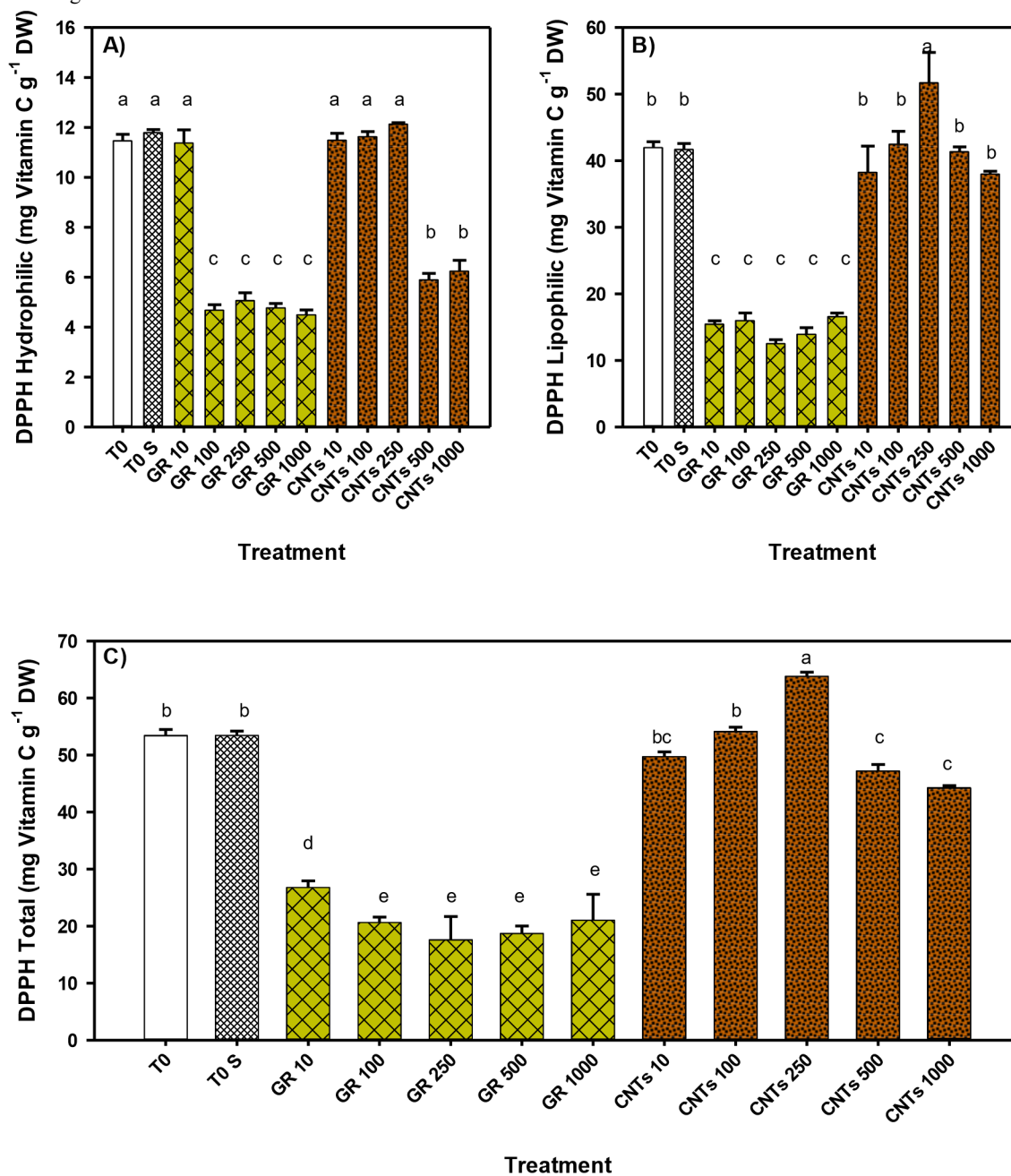


Figure 5. The antioxidant capacity determined in the leaves of tomato seedlings treated with carbon nanomaterials. Each data point is the average of five replicates \pm standard error. Different letters indicate significant differences between treatments according to Fisher's least significant difference test ($p \leq 0.05$). T0: absolute control. T0 S: sonicated control. GR: graphene. CNTs: carbon nanotubes. DPPH: 2,2-difenil-1-picirilhidracilo (equivalents of vitamin C mg g⁻¹ DW). H: hydrophilic compounds. L: lipophilic compounds. DPPH Total: total antioxidant capacity.

The enzymatic activity evaluated in the different enzymes showed significant differences between treatments, where in all cases, at least one treatment with CNMs was greater than the absolute control (Figure 6). The PAL enzyme showed a greater activity with the CNTs 250 treatment, with an increase of 24% compared to the absolute control, while the rest of the concentrations of CNTs were statistically equal to the absolute control. On the contrary, the addition of graphene presented a negative effect, as the activity of this enzyme decreased in all the evaluated concentrations (Figure 6E). The activity of the PAL enzyme is of the utmost importance because it is the first enzyme in the phenylpropanoid pathway that catalyzes the deamination of phenylalanine to cinnamic acid to produce phenolic compounds [68]. The phenolic compounds present a variety of functions in plants, including an antioxidant effect; therefore, changes in the activity of PAL can also influence protection against oxidative stress.

Regarding the activity of the antioxidant enzymes, the treatment with 250 mg L⁻¹ of CNTs increased the APX activity by 50%, while the highest dose (1000 mg L⁻¹) generated a decrease of 41% in comparison to the absolute control (Figure 6A). The treatments with the application of graphene did not show differences with respect to the absolute control. The enzymatic activity of glutathione peroxidase (GPX) was affected to a greater extent by the application of graphene, as it was increased 179% and 170% with the GR 100 and 250 treatments, respectively, in comparison to the absolute control.

The CNTs also had a positive effect, with the CNTs 250 treatment being the one with the highest increase at 55% more than the absolute control (Figure 6B). The activity of the catalase enzyme was increased in all graphene doses, and, with the exception of the lowest dose of CNTs (10 mg L⁻¹), the rest of the treatments also increased the activity of the enzyme. The treatment of CNTs 250 generated the greatest increase in catalase activity at 79% more than the absolute control (Figure 6C). The activity of SOD increased to a greater extent with high doses of both CNMs, where the GR 1000 treatment showed 32% more activity than the absolute control. The treatment of CNTs 1000 was 29% more (Figure 6D). The results indicated that the CNTs 250 treatment had the greatest influence on the enzymatic activity, as it was the best for PAL, APX, and catalase (CAT), and it was statistically equal to the best treatment in GPX and SOD (Figure 6).

The importance of the different antioxidant enzymes that were evaluated in the present study is due to their active participation in ROS neutralization, which allows for the maintenance of ROS homeostasis in plants. The enzyme SOD and its isoenzymes (Mn-SOD, Cu/Zn-SOD, and Fe-SOD) convert the O₂^{•-} to H₂O₂ and O₂, whereas the enzymes APX, GPX, and CAT participate in the transformation of H₂O₂ to H₂O. APX requires ascorbic acid and reduced glutathione as substrates, while GPX uses GSH as a reducing agent [69]. CAT presents a high affinity and ability to dismutate H₂O₂ molecules (mainly in the peroxisome) in water, oxygen, and, to a lesser degree, organic peroxides without requiring a reducing compound [70].

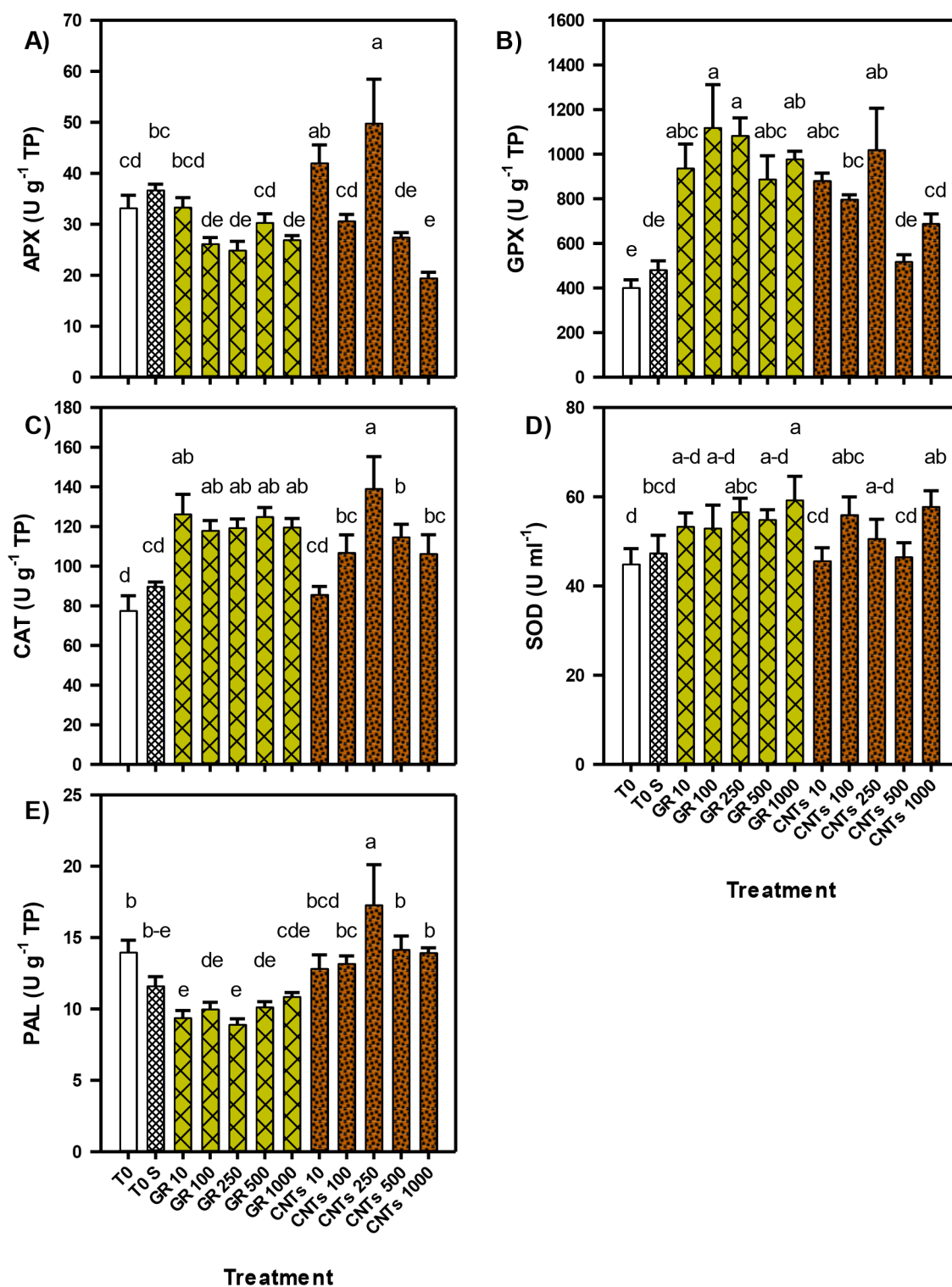


Figure 6. Enzymatic activity in leaves of tomato seedlings treated with carbon nanomaterials. Each data point is the average of five replicates \pm standard error. Different letters indicate significant differences between treatments according to Fisher's least significant difference test ($p \leq 0.05$). T0: absolute control. T0 S: sonicated control. GR: graphene. CNTs: carbon nanotubes. PAL: phenylalanine ammonia lyase. APX: ascorbate peroxidase. GPX: glutathione peroxidase. SOD: superoxide dismutase. CAT: catalase. TP: total proteins.

Other authors have also reported that CNMs influence the activity of antioxidant enzymes. Zhao et al. [71] reported that the CNTs (0, 0.45, 0.9, 2.25, and 4.5 mg L⁻¹), evaluated in an MS culture medium for 25 days, increased the CAT, SOD, and APX contents in *Arabidopsis*. Lin et al. [47] mentioned that the application of CNTs in cell culture in *Arabidopsis* T87 in a range of 10–600 mg L⁻¹ decreased the enzymatic activity of SOD.

The different responses that have been observed with CNMs are due to the ability of cells to penetrate the seed layer and to be internalized in the different organelles of the cells [14,26], either through endocytosis, pore formation, transport proteins, or plasmodesmata [72]. Once inside, CNMs stimulate the production of ROS through interactions with cellular organelles [65]. This is due to the fact that nanomaterials have a corona around their surface with a high density of surface charges that, when they interact with cells, modify the integral activity of the proteins, generating a cellular response [6]. These responses can vary from biostimulation to cell death depending on the level of oxidative stress generated by the increase in ROS.

As shown in Figure 7, there was a high correlation between some compounds of the antioxidant system of tomato seedlings. The chlorophylls showed a positive correlation with β -carotene, which may have been related to the function of this accessory pigment compound acting as antenna molecules and capturing light in chloroplasts [57,58]. In addition to this, one of the main role of β -carotene is the extinction of ³Chl*, thus providing the inhibition of production and damage of ¹O₂ [59], that would be caused by stress conditions. All of these compounds showed a negative correlation with the antioxidant capacity.

Researchers have also observed that there is a high correlation between the antioxidant capacity and the PAL enzyme. This is an expected response due to the role of said enzyme in the production of phenolic compounds [68], which, among other things, function as antioxidants and protect against oxidative stress.

In the case of hydrogen peroxide, a negative correlation with GSH was observed, which was likely derived from the role it has in the control and detoxification of ROS [60].

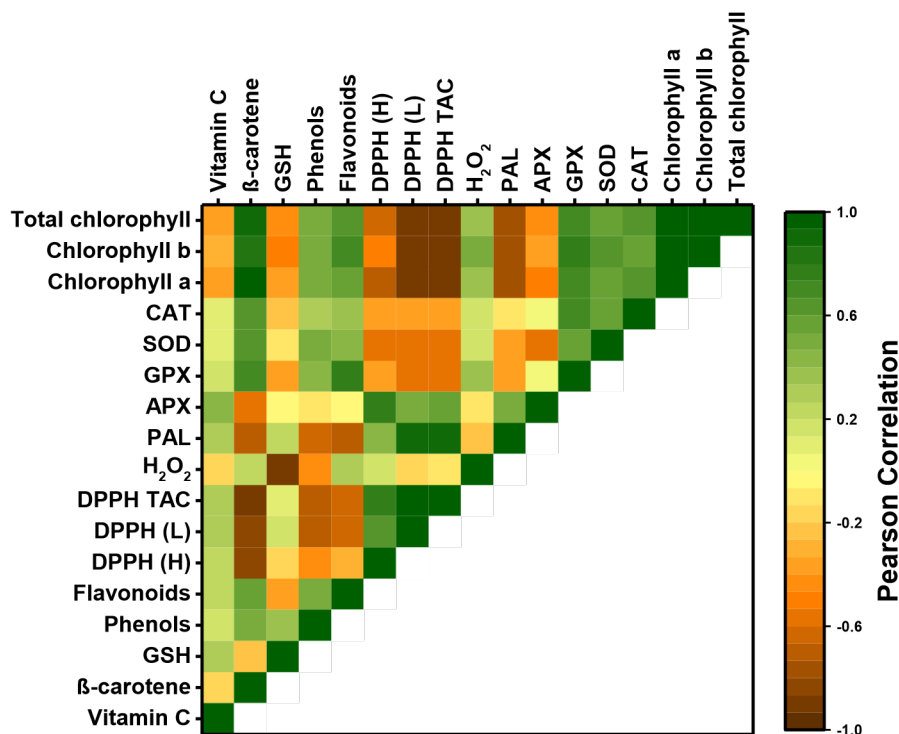


Figure 7. The Pearson correlations of antioxidant variables determined in the leaves of tomato seedlings treated with carbon nanomaterials.

4. Conclusions

Seed priming with CNMs did not affect the germination of tomato plants. Only high doses induced a negative effect. However, the CNMs negatively affected the length of the root and the fresh weight of the hypocotyl, and they promoted the growth of the root. Seed priming with CNMs induced significant changes in the growth of seedlings in a concentration-dependent manner. The vigor of the tomato seedlings was generally promoted with graphene and CNTs in low doses. However, the high doses of both CNMs had negative effects. Therefore, it is important to consider the concentrations used in order to obtain favorable results in the growth of seedlings.

Seed priming with graphene favored the increase of chlorophylls, as well as the contents of proteins and non-enzymatic antioxidants (vitamin C, β -carotene, glutathione, phenols, and flavonoids) of tomato seedlings. However, the antioxidant capacity was greater with the use of CNTs for seed priming. Likewise, both CNMs promoted enzymatic activity; the CNTs increased the PAL, APX and CAT enzymes, while GPX and SOD were greater with graphene. Therefore, seed priming with CNMs had pronounced effects on the antioxidant system of the tomato plants, presenting different responses depending on whether graphene or carbon nanotubes were used.

The seed priming with carbon nanomaterials induced favorable responses that could potentially improve the development of the tomato crop. These results indicated that the treatment of tomato seeds with carbon nanomaterials could be a good option to induce biostimulation, as well as demonstrating an easy method of application.

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ARTÍCULO 2

**Seed Treatment with Carbon Nanomaterials Impacts Growth and Nutrient
Absorption in Tomatoes Under Saline Stress**

El Tratamiento de Semillas con Nanomateriales de Carbono Impacta en el Crecimiento y Absorción de Nutrientes en Tomate Bajo Estrés Salino

Seed Treatment with Carbon Nanomaterials Impacts Growth and Nutrient Absorption in Tomatoes Under Saline Stress

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Resumen

En el presente estudio, se evaluaron los efectos del tratamiento de semillas de tomate con nanotubos de carbono (CNT) y grafeno (GP), a concentraciones de 50, 250 y 500 mg L⁻¹ y dos controles (sin sonicar y sonicado), en el crecimiento, desarrollo y la absorción mineral en plantas de tomate sin estrés salino (Sin NaCl) y con estrés salino (50 mM NaCl). La aplicación de GP y CNT en plantas sin estrés salino no afectó la mayoría de los parámetros morfológicos, como el peso promedio de frutos y el rendimiento. Las biomásas frescas y secas tanto de raíz como de parte aérea fueron modificadas por los nanomateriales de carbono (CNMs). Por otro lado, la altura de las plantas bajo salinidad aumentó significativamente con el tratamiento de GP y CNT en la dosis más baja (50 mg L⁻¹). Mientras que el diámetro de tallo disminuyó notablemente. El número de frutos con pudrición apical y el % de daño fueron similares a los controles. Además, el tratamiento con GP y CNT modificó la concentración de macro y micro nutrientes en las hojas y frutos de las plantas de tomate. La aplicación de GP y CNT a las semillas en sus diferentes concentraciones puede generar respuestas positivas en el desarrollo y crecimiento de las

plantas, y bajo condiciones de estrés salino pueden inducir respuestas benéficas al mejorar la absorción de los nutrientes.

Palabras clave: grafeno, nanotubos de carbono, salinidad, macronutrientes, micronutrientes.

Abstract

In the present study, the effects of the treatment of tomato seeds with carbon nanotubes (CNT) and graphene (GP), at concentrations of 50, 250 and 500 mg L⁻¹ and two controls (without sonication and sonicated) in growth, development and mineral absorption in tomato plants were evaluated. Two conditions of saline stress were considered: without saline stress (No NaCl) and with saline stress (50 mM NaCl). The application of GP and CNT in plants without saline stress did not affect most of the morphological parameters, such as average fruit weight and yield. The fresh and dry biomasses, both root and aerial, were modified by carbon nanomaterials (CNMs). On the other hand, the height of the plants under salinity increased significantly with the treatment of GP and CNT at the lowest dose (50 mg L⁻¹). While the DT decreased notably. The number of fruits with blossom end rot and the % fruits with damage were similar to the controls. In addition, treatment with GP and CNT modified the concentration of macro and micro nutrients in the leaves and fruits of tomato plants. The application of GP and CNT to the seeds in their different concentrations can generate positive responses in the development and growth of the plants, it has positive effects and under conditions of saline stress they can induce beneficial responses by improving the absorption of nutrients.

Keywords: graphene, carbon nanotubes, salinity, macronutrients, micronutrients.

Introducción

La salinización de los recursos de suelo y agua va en aumento debido al uso irracional de insumos agrícolas para incrementar la producción agrícola (Arif et al., 2020; Phogat et al., 2020). A nivel mundial, la salinidad induce un estrés de tipo abiótico que afecta entre un cuarto y un tercio de la productividad de los cultivos (Munns et al., 2019). Aproximadamente el 10% de la superficie terrestre mundial y el 50% de las áreas irrigadas están expuestas a la salinidad, lo que provoca una pérdida de aproximadamente 12 mil

millones de dólares en el sector agrícola (Kamran et al., 2020; Singh et al., 2020). Un suelo con una conductividad eléctrica de 4 dS m^{-1} (aproximadamente 40 mM NaCl), un estrés osmótico de 0.2 MPa y un porcentaje de sodio intercambiable de 15% a 25% se denomina suelo afectado por sal (Kosová et al., 2013).

La salinidad induce un amplio espectro de alteraciones fisiológicas (conductancia estomática, tasa de transpiración y fotosíntesis) biométricas (altura, área foliar, producción de biomasa) y bioquímicas (enzimas antioxidantes), y puede provocar estrés iónico, estrés osmótico y estrés oxidativo en las plantas (Machado et al., 2020). El estrés iónico es causado por una mayor acumulación de iones de sal en las células de la planta a niveles tóxicos, y el estrés osmótico es causado por una disminución en el potencial osmótico del agua, además, el estrés iónico provoca una deficiencia de nutrientes, perturba el equilibrio de las especies reactivas de oxígeno (ROS) en las células de las plantas, lo que causa directamente el estrés oxidativo (Hernández, 2019; Hussain et al., 2020).

Los nutrientes minerales como nitrógeno (N), fósforo (P), potasio (K), calcio (Ca), magnesio (Mg), azufre (S), zinc (Zn) y boro (B), entre otros, son esenciales para la productividad del cultivo en condiciones de estrés salino (Zörb et al., 2019), por lo que una deficiencia de éstos nutrientes es un problema adicional ya que incluye una menor acumulación de biomasa, una mayor susceptibilidad a patógenos y enfermedades, y un retraso en el crecimiento de las plantas directamente relacionado con el rendimiento de los cultivos (Farooq et al., 2017). Cabe mencionar, que las plantas son inherentemente dinámicas y flexibles en su metabolismo, lo que puede propiciar una adaptación a ambientes salinos (Arsova et al., 2019), para ello, dependen de señales y vías que restablezcan la homeostasis de las especies iónicas, osmóticas y ROS (Ma and Yan, 2018; Sewelam et al., 2016).

Por otro lado, el tomate es miembro de la familia de las solanáceas y es el cultivo de mayor valor en el mundo (Kayess et al., 2020), por ser rico en moléculas antioxidantes como carotenoides, vitamina E, vitamina C, ácido ascórbico y compuestos fenólicos, principalmente flavonoides (Devkar et al., 2019). Se considera moderadamente sensible al estrés salino, por lo que dicho estrés representa una amenaza sustancial para su

producción, debido a los efectos negativos ocasionados (Kashyap et al., 2020; Singh et al., 2020).

En este contexto, los avances de la nanotecnología proporcionan herramientas novedosas para el sector agroalimentario, una de éstas herramientas son los nanomateriales (NMs). El uso de los NMs en los cultivos agrícolas, producen respuestas morfológicas, fisiológicas y bioquímicas que pueden ayudar a la planta a tolerar algún tipo de estrés ya sea de tipo biótico o abiótico, al generar cambios en el transcriptoma, proteoma, metaboloma e ionoma (Wang et al., 2019), además, puede mejorar la absorción de agua y nutrientes (Sanzari et al., 2019). Recientemente, los nanomateriales a base de carbono (CNMs) se han aplicado como reguladores del crecimiento de las plantas, agentes de control de plagas, nanosensores para la detección de plagas y portadores de nutrientes en la agricultura (Mukherjee et al., 2016). Esto se debe a la capacidad de translocación que depende del tamaño y la carga superficial de los mismos (carga negativa), promoviendo una serie de respuestas fisiológicas y bioquímicas que mejoran el crecimiento de la planta y la protección de los cultivos (Joshi et al., 2020). La eficacia de un tipo particular de CNMs varía de una planta a otra y el resultado (nulo, beneficioso, o adverso) de las interacciones CNMs-planta, depende de la carga, tamaño, forma, concentración, cantidad y tiempo de exposición (Verma et al., 2019). Dentro de estos CNMs destacan los nanotubos de carbono (CNT) de pared simple (SWCNT) y de pared múltiple (MWCNT), así como el grafeno (GP), los cuales se han aplicado para mejorar el crecimiento de las plantas (Husen and Siddiqi, 2014).

Algunos de éstos CNMs se han utilizado en el tratamiento de semillas y tienen un impacto positivo en la mejora del crecimiento de las plantas (Ratnikova et al., 2015), que van desde el mejoramiento en la germinación de semillas hasta el incremento en la productividad y el rendimiento de los cultivos (Gao et al., 2020). Se ha reportado que el tratamiento de semillas a través de la imbibición con algunos CNMs, como los CNT, pueden romper la testa de la semilla y crear poros para ingresar dentro de la semilla (Khodakovskaya et al., 2009; Ratnikova et al., 2015). Gilbertson et al., (2020), mencionan que a bajas concentraciones, activan el canal de acuaporinas y se promueve la absorción de agua y

nutrientes. Por el contrario, en dosis altas, promueven la producción de radicales libres que inducen un estrés oxidativo y daño celular (Samadi et al., 2021).

En este sentido, la exposición directa de las semillas con los CNMs puede romper la latencia de las semillas y mejorar la germinación de las mismas, ya que induce una abrasión del endocarpio y aumenta la infiltración de oxígeno y humedad (Sayedena et al., 2018). Joshi et al. (2018), reportó un crecimiento más rápido y mejoras en el rendimiento del cultivo de trigo al tratar las semillas con MWCNTs (0, 70, 80 y 90 mg L⁻¹) debido a una mejor absorción de agua y minerales esenciales como P y K. Otro estudio menciona que las plantas de arroz tratadas con MWCNTs (70, 80 y 90 mg L⁻¹) desde la semilla, tienen un crecimiento más rápido, y además, una mejor absorción de agua y nutrientes, por lo que se obtiene un incremento en el rendimiento del cultivo (Joshi et al., 2020). Con lo anterior, se asume que la aplicación de CNMs en la semilla puede mejorar la fisiología de la planta, y además, funcionar como elicitores para inducir tolerancia a un estrés, en este caso estrés por NaCl. Con lo anterior, el presente estudio tiene como objetivo de evaluar diferentes concentraciones de GP y CNT en el crecimiento y la absorción mineral de nutrientes en plantas de tomate cultivadas bajo condiciones de estrés salino.

Materiales y métodos

Material vegetal

Las semillas utilizadas en el presente estudio fueron de tomate híbrido “Pony Express F1” (Harris Moran, Davis, CA, USA), tipo saladette y crecimiento determinado.

Nanomateriales de carbono

Los CNMs utilizados fueron: nanotubos de carbono (CNT) y grafeno (GP). Los CNT fueron multicapa, con una pureza de 95%, un diámetro de 30-50 nm y de 10 a 20 µm de largo (Nanostructured & Amorphous Materials, Inc.). El grafeno (GP) tiene una pureza del 97%, un diámetro de 2 µm, un grosor de 8 a 12 nm y con 10-12 capas (Cheap Tubes Inc.).

Tratamiento de semillas

Los tratamientos consistieron en tres diferentes concentraciones: 50, 250 y 500 mg L⁻¹ de GP y CNT, respectivamente. Éstas concentraciones fueron seleccionadas en un rango de dosis baja, media y alta, de acuerdo a los resultados obtenidos en el crecimiento y desarrollo de las plantas de tomate realizados en un estudio previo con los mismos CNMs (López-Vargas et al., 2020). Las soluciones de los tratamientos fueron preparadas en vasos de precipitados de 50 ml, que contenían 20 ml de cada tratamiento y 40 semillas de tomate en cada vaso, posteriormente fueron sonicadas por 10 minutos a una amplitud de vibración de 60% a 20 Khz en un ultrasonicador (sonicador Q500, QSONICA, Melville, NY, EE. UU.), similar a lo reportado por Ratnikova et al., (2015). Las semillas tratadas fueron almacenadas a temperatura ambiente (25 ± 1 °C) con 16 h de luz y 8 de oscuridad durante 24 h en frascos de vidrio con tapa y agitados cada 8 hrs para evitar la precipitación de los CNMs y asegurar la imbibición en las semillas (Ratnikova et al., 2015). También se evaluaron dos controles que contenían agua destilada con semillas sin sonicar (CTRL NS) y agua destilada con semillas sonicadas (CTRL S).

Desarrollo del cultivo

Transcurrida las 24 hrs, la siembra de las semillas tratadas fue realizada en charolas de poliestireno previamente etiquetadas. El trasplante fue realizado a los 30 días después de la siembra (dds) en bolsas de polietileno color negro con capacidad de 14 L. El sustrato utilizado fue una mezcla de perlita-peat moss en proporción 1:1. El experimento se dividió en dos (experimento 1 y experimento 2) y fueron establecidos por separado: se trasplantaron 16 plantas por cada tratamiento para el experimento 1 y 16 plantas por tratamiento para el experimento 2, considerando una planta como unidad experimental (Tabla 1). El sistema de riego fue dirigido, a los 8 días después del trasplante (ddt), las plantas del experimento 1 fueron irrigadas con solución nutritiva Steiner (1961) y las plantas del experimento 2 fueron irrigadas con solución nutritiva Steiner combinada con 50 mM de cloruro de sodio (NaCl), dichas soluciones fueron preparadas en tinacos diferentes con capacidad de 1100 L. La conductividad eléctrica (CE) de las soluciones fue monitoreada durante el ciclo y éstas oscilaban entre 1.9-2.5 μ S para la solución Steiner normal y 5.5-7.5 μ S para la solución Steiner con NaCl. El pH se ajustó a 6.5 con ácido

sulfúrico concentrado en ambos tinacos para favorecer la absorción de nutrientes. El cultivo fue manejado a un solo tallo, y se desarrolló por 160 ddt.

Tabla 1. Tratamientos con GP, CNT y NaCl a semillas de tomate.

Tratamiento	Concentración (mg L ⁻¹)	Experimento 1	Experimento 2
CTRL NS	0	Sin NaCl	50 mM de NaCl
CTRL S	0	Sin NaCl	50 mM de NaCl
GP	50	Sin NaCl	50 mM de NaCl
	250	Sin NaCl	50 mM de NaCl
	500	Sin NaCl	50 mM de NaCl
CNT	50	Sin NaCl	50 mM de NaCl
	250	Sin NaCl	50 mM de NaCl
	500	Sin NaCl	50 mM de NaCl

Evaluación de parámetros agronómicos

Para la evaluación del crecimiento y desarrollo de las plantas de tomate, se realizaron mediciones a los 15, 30, 45, 60 y 75 días después de la aplicación de NaCl. La altura de la planta se midió con un flexómetro, el diámetro de tallo fue determinado con un vernier digital, además, el número de hojas, número de racimos, número de frutos por planta, fueron contabilizados. En el caso de las plantas desarrolladas con NaCl, se contabilizó el número de frutos dañados con pudrición apical (“blossom end root”) por cada planta para determinar el porcentaje de daño, y se evaluó rendimiento. La biomasa fresca de parte aérea y raíz (g), fue determinada utilizando una balanza digital (OHAUS modelo Adventurer Pro). La biomasa seca se obtuvo al secar las muestras en una estufa de secado marca Drying Oven modelo DHG9240A durante 72 h a una temperatura constante de 70°C.

Contenido mineral

El contenido de macronutrientes (P, K, Ca, Mg, S y Na) y micronutrientes (Fe, Cu, Zn, Mn, Mo y B) en hojas y frutos fue determinado con un espectrofotómetro de emisión de

plasma (Optima 8300 ICP-OES Optical System, PerkinElmer, MA, USA) siguiendo la metodología descrita por Hernández-Hernández et al., (2018). Para el análisis de tejido seco de hojas y frutos, se tomó 1 g de cada muestra, los cuales fueron digeridos en 30 ml de ácido nítrico a 300°C durante 6 horas, y aforado a 50 ml con agua desionizada para su posterior análisis.

Análisis estadístico

El experimento se estableció en un diseño completamente aleatorizado. El análisis estadístico se realizó de manera independiente para cada experimento. En las variables agronómicas se consideraron 16 repeticiones por tratamiento. Para las variables fisicoquímicas y bioquímicas se consideraron seis repeticiones por tratamiento. El análisis de varianza y la prueba de medias Fisher LSD ($\alpha=0.05$) se realizó en el software Infostat (v2018) (<https://www.infostat.com.ar>).

Resultados

Variables agronómicas

La adición de GP y CNT en las plantas sin estrés salino no afectó la altura de las plantas (Fig. 1A). Bajo estrés salino, las diferentes dosis de GP y CNT aplicadas a las plantas no afectaron la altura de las plantas, ya que los tratamientos fueron similares al CTRL NS. Sin embargo, al compararlos con el CTRL S, la altura de las plantas se vio favorecida con la adición de GP a 50 y 250 mg L⁻¹ presentando un incremento de 11.04% y 12.47%, respectivamente, y 11.34% con la aplicación de CNT a 250 mg L⁻¹ (Fig. 1A).

El diámetro de tallo de las plantas sin salinidad se incrementó 4.57% y 9.76% con CNT a 50 y 250 mg L⁻¹, respectivamente, en comparación con el CTRL NS. Ninguna concentración de GP afectó esta variable. No obstante, al comparar los tratamientos con el CTRL S, disminuyó el diámetro de tallo con la adición de GP en sus diferentes dosis (10.60%, 7.26% y 6.53%, respectivamente). De igual manera los CNT disminuyeron esta variable con las dosis de 50 y 500 mg L⁻¹ (4.73% y 6.20%, respectivamente) (Fig. 1B). Cabe mencionar que al comparar ambos controles se observó que el proceso de sonicado induce un incremento del diámetro de tallo de 9.76%. Mientras que el diámetro de tallo de las plantas con salinidad disminuyó con la adición de GP en sus diferentes dosis en un

rango de 4.62-5.07%, en comparación con el CTRL NS; y en un rango de 6.98-7.42% en comparación con el CTRL S. La adición de CNT a 250 mg L⁻¹ disminuyó 6.25% y 8.57% en comparación con ambos controles, respectivamente (Fig. 1B).

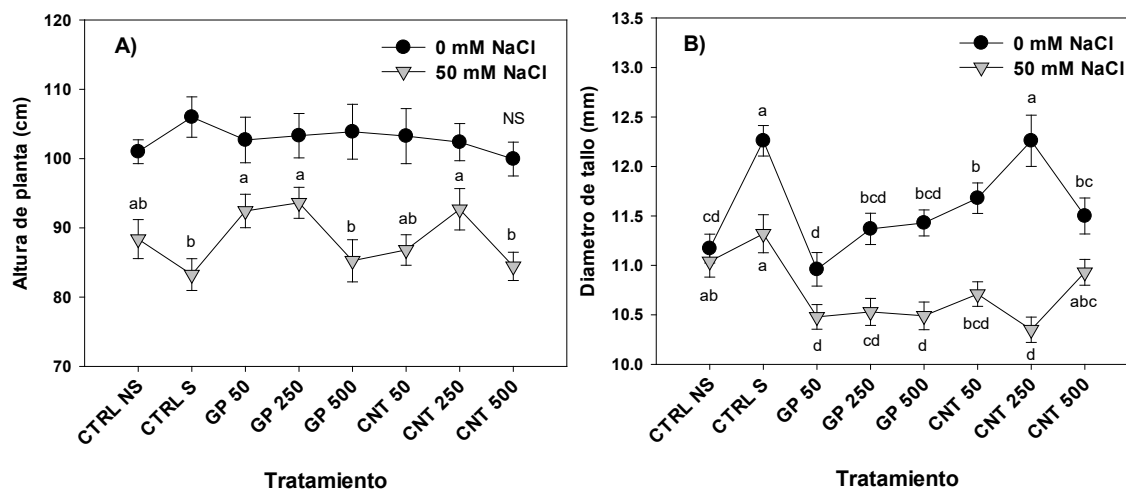


Figura 1. Altura de planta (A) y diámetro de tallo (B) de las plantas tratadas con CNMs y NaCl. Diferentes letras indican diferencia significativa entre tratamientos de acuerdo a LSD Fisher ($\alpha = 0.05$). ns: no significativo; $n = 16 \pm$ error estándar.

El peso promedio de los frutos (Fig. 2A) así como el rendimiento de frutos por planta (Fig. 2B) no fueron afectados por la adición de GP y CNT en plantas sin estrés salino y ni con estrés salino. Sin embargo, se puede observar un ligero incremento de alrededor del 8.5%, en el rendimiento y peso promedio de fruto de las plantas estresadas por salinidad con el tratamiento GP a 50 mg L⁻¹ en comparación al CTRL NS.

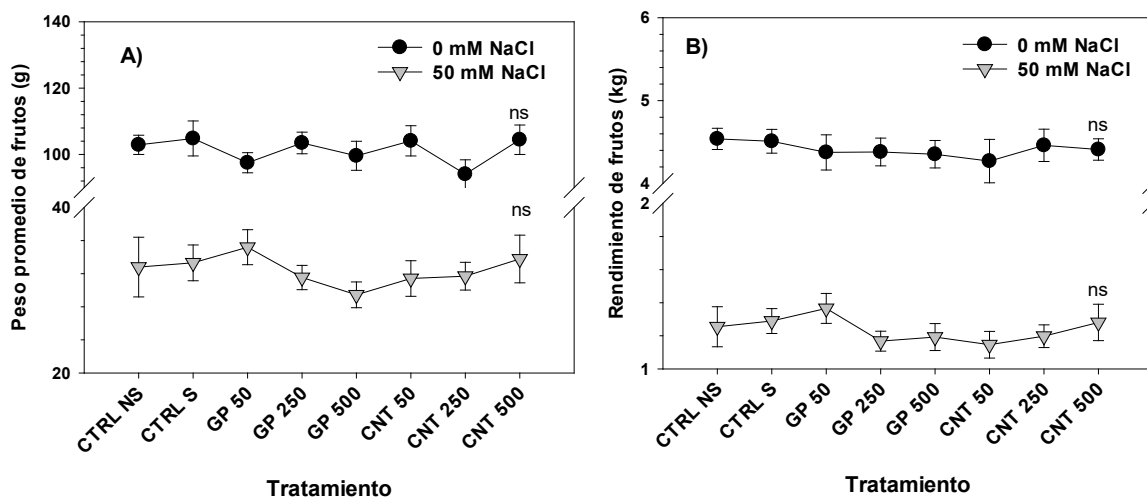


Figura 2. Peso promedio de frutos (A) y rendimiento de frutos (B) de las plantas tratadas con CNMs y NaCl. Diferentes letras indican diferencia significativa entre tratamientos de acuerdo a LSD Fisher ($\alpha = 0.05$). ns: no significativo; $n = 16 \pm$ error estándar.

El número de frutos dañados por pudrición apical en las plantas bajo estrés salino no presentó diferencias entre tratamientos (Fig. 3). De igual manera el porcentaje (%) de frutos dañados por planta no fue afectado al ser comparados con ambos controles (Fig. 3). Sin embargo, se observa que el tratamiento GP a 500 mg L^{-1} presentó el menor porcentaje y menor número de frutos dañados en plantas bajo estrés salino.

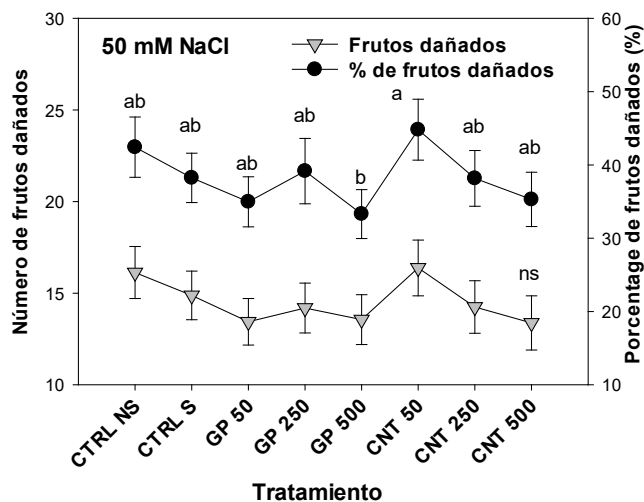


Figura 3. Número de frutos dañados por pudrición apical y porcentaje de frutos dañados (%) de las plantas tratadas con CNMs y NaCl. Diferentes letras indican diferencia significativa entre tratamientos de acuerdo a LSD Fisher ($\alpha = 0.05$). ns: no significativo; $n = 16 \pm$ error estándar.

El peso fresco aéreo (PFA) de las plantas sin estrés salino no presentó diferencias significativas entre tratamientos. Sin embargo, el proceso de sonicado incrementó el PFA en un 14.12%, en comparación a no sonicar. Además, la aplicación de CNT a 500 mg L^{-1} presentó una disminución del PFA de 21.58% en comparación al CTRL S (fig. 4 A). En las plantas con estrés salino, la adición de GP a 500 mg L^{-1} disminuyó 24.20% el PFA comparado con el CTRL NS, y comparado con el CTRL S disminuyó 18.09%. El tratamiento CNT a 50 mg L^{-1} incrementó 15.20% el PFA en comparación con el CTRL S (Fig. 4A).

El peso seco aéreo (PSA) de las plantas sin estrés salino se incrementó con los tratamientos GP y CNT a 500 y 250 mg L^{-1} en 17.87% y 16.20%, respectivamente, en comparación con el CTRL NS (Fig. 4 B). En las plantas con estrés salino, el PSA disminuyó 18.24% con el tratamiento de GP a 500 mg L^{-1} y 18.87% con el CTRL S, en comparación con el CTRL NS (Fig. 4B).

La adición de GP y CNT a las plantas sin estrés salino no afectó el peso fresco (PFR) o seco de raíz (PSR) (Fig. 4). Sin embargo, bajo estrés salino el PFR y PSR se observó un incremento con la aplicación de CNT, sobre todo con CNT a 500 mg L^{-1} con un 65.69% más PFR y 33.48% más PSR en comparación con el CTRL NS (Fig. 4).

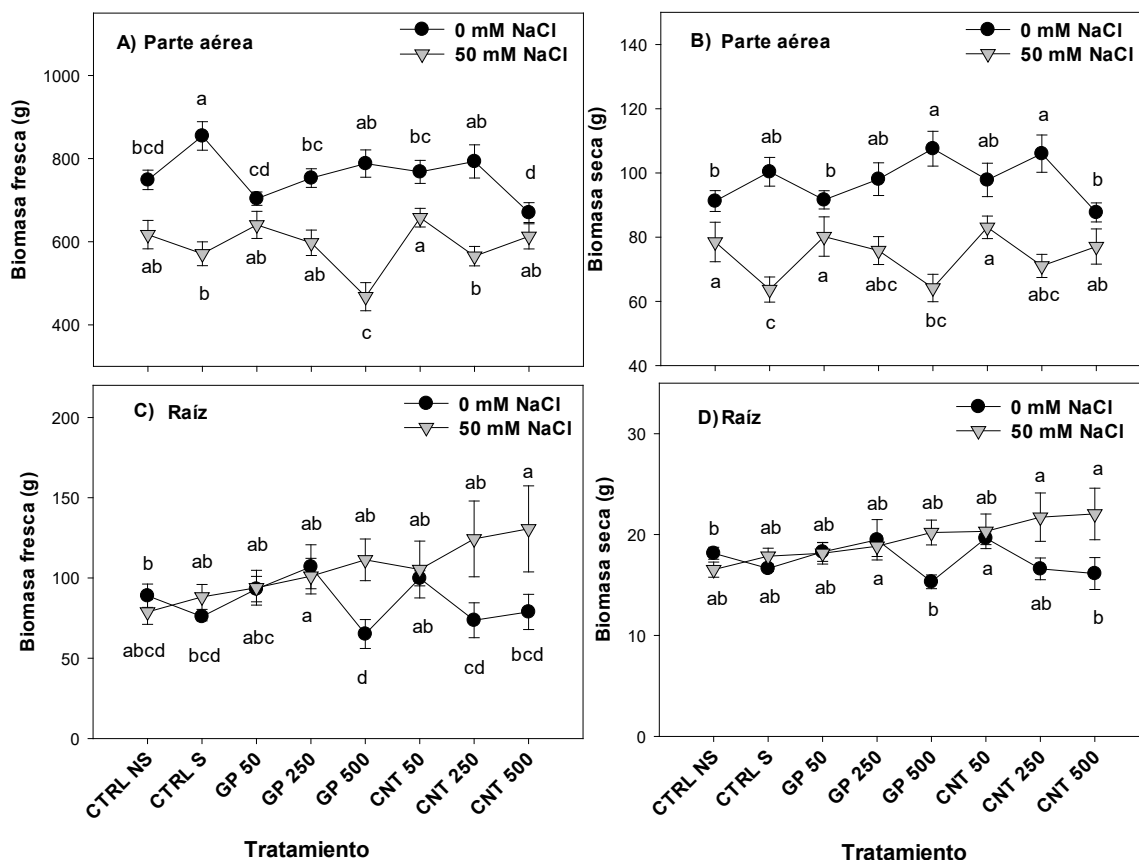


Figura 4. Biomasa fresca (A, C) y seca (B, D) de parte aérea (A, B) y raíz (C, D) de las plantas tratadas con con CNMs y NaCl. Diferentes letras indican diferencia significativa entre tratamientos de acuerdo a LSD Fisher ($\alpha = 0.05$). ns: no significativo; $n = 16 \pm$ error estándar.

Contenido de nutrientes en hojas y frutos de tomate

El contenido de macronutrientes en los diferentes órganos de las plantas de tomate tratadas con CNMs combinados con estrés salino (0 y 50 mM NaCl) fue diferente. En el contenido de P en las hojas no se tuvo efecto por la aplicación de CNMs en ninguna condición de estrés salino (Fig. 5A). En los frutos de plantas sin estrés salino, el P presentó una disminución con la aplicación de los CNMs, sobre todo con los tratamientos GP y CNT a 500 y 250 mg L⁻¹, respectivamente. Sin embargo, en los frutos de plantas con estrés salino no se afectó el contenido de P por los tratamientos (Fig. 5B). Mientras que el estrés salino consistentemente influye negativamente en el contenido de P en hojas y frutos (Figs. 5A y B).

El contenido de K en hojas de plantas sin estrés salino se incrementó en 22.84% y 28.61% con CNT a 250 y 500 mg L⁻¹ en comparación con el CTRL NS. Bajo estrés salino el tratamiento CNT a 250 mg L⁻¹ indujo el mayor incremento de K en las hojas, 40.75% más que el CTRL NS (Fig. 5C). En los frutos de plantas sin estrés salino se observó una disminución de K con los tratamientos GP y CNT a 500 y 250 mg L⁻¹, siendo 24.98% y 27.79% menos que el CTRL S. En los frutos de plantas con estrés salino no hubo diferencias entre tratamientos (Fig. 5D).

El contenido de Ca solo fue afectado por los CNMs en los frutos de plantas sin estrés salino, donde se observó una disminución con los tratamientos GP y CNT a 500 y 250 mg L⁻¹ (34.45% y 37.81%, respectivamente, en comparación al CTRL NS) (Fig. 5F). El contenido de Ca en las hojas no presentó diferencias entre tratamientos (Fig. 5E).

El contenido de Mg en hojas de plantas sin estrés salino se incrementó en 52.87% y 49.71%, con los tratamientos GP y CNT a 50 mg L⁻¹, respectivamente, en comparación al CTRL S. Bajo estrés salino, no se observaron diferencias entre tratamientos (Fig. 5G). En los frutos de plantas sin estrés salino se observó que los tratamientos GP a 500 mg L⁻¹ y CNT a 250 y 500 mg L⁻¹, disminuyeron el contenido de Mg en comparación al CTRL NS (27.48%, 19.08, 21.37%, respectivamente). En los frutos de plantas con estrés salino se observó un incremento de Mg de 22.35% con el tratamiento GP a 250 mg L⁻¹ en comparación al CTRL NS (Fig. 5H).

El contenido de S en las hojas de plantas sin estrés salino disminuyó 22.12% con el tratamiento CNT a 500 mg L⁻¹ en comparación al CTRL S. En las hojas de plantas con estrés salino no hubo diferencias entre tratamientos (Fig. 5I). En los frutos de plantas sin estrés salino disminuyó 34.65% con el tratamiento CNT a 250 mg L⁻¹ en comparación al CTRL NS. En los frutos de plantas con estrés salino no hubo diferencias entre tratamientos (Fig. 5J).

El contenido de Na en las hojas sin estrés salino no se modificó por los tratamientos de CNMs. Sin embargo, en las hojas de plantas con estrés salino el Na se incrementó 82.87% con el tratamiento GP a 500 mg L⁻¹ en comparación al CTRL NS (Fig. 5K). En los frutos de plantas sin estrés no hubo diferencias entre tratamientos. Y en frutos de plantas con estrés salino el contenido de Na se incrementó 45.29% con el tratamiento GP a 250 mg L⁻¹

¹ en comparación al CTRL NS. Sin embargo, el tratamiento de CNT a 500 mg L⁻¹ disminuyó 42.01% el contenido de Na en comparación al CTRL S (Fig. 5L).

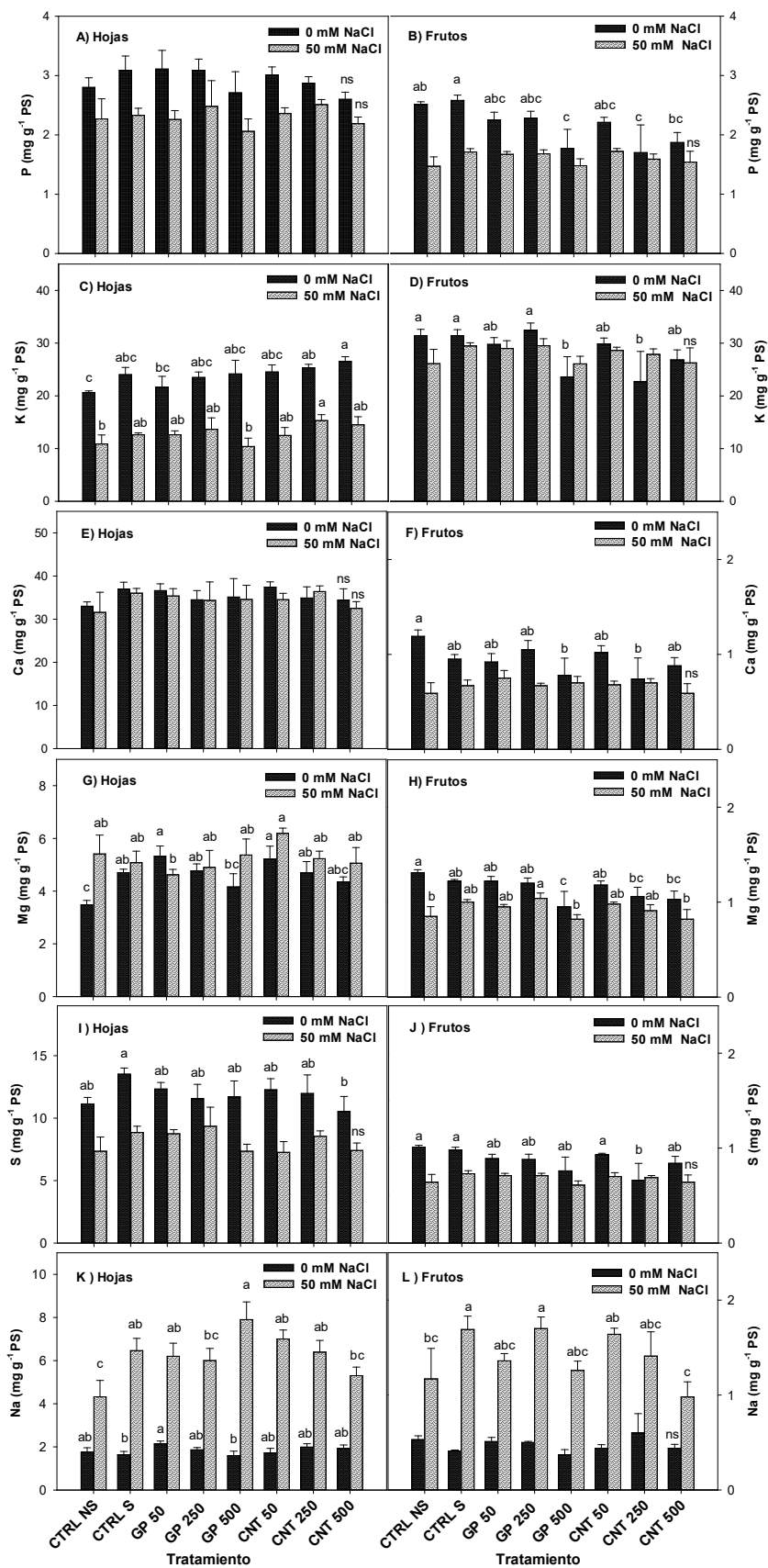


Figura 5. Contenido de macronutrientes en hojas y frutos de las plantas tratadas con CNMs y NaCl. Diferentes letras indican diferencia significativa entre tratamientos de acuerdo a LSD Fisher ($\alpha = 0.05$). ns: no significativo; $n = 6 \pm$ error estándar.

Los micronutrientes en las hojas y frutos de las plantas de tomate presentaron diferencias significativas entre tratamientos. La concentración de Fe en las hojas de las plantas de tomate no se modificó por los tratamientos en ninguna condición de estrés (Fig. 6A). En los frutos de plantas sin estrés salino el contenido de Fe se incrementó significativamente con el tratamiento CNT a 500 mg L^{-1} , siendo 141.05% más que el CTRL NS. En los frutos de plantas con estrés salino el tratamiento GP a 250 mg L^{-1} incrementó 250.76% el contenido de Fe en comparación al CTRL NS (Fig. 6B).

El contenido de Cu en las hojas de plantas sin estrés salino fue disminuido por el tratamiento de GP a 50 mg L^{-1} en comparación del CTRL NS. En las hojas de plantas con estrés salino no hubo diferencias en el contenido de Cu; sin embargo, se observó que la concentración de este micronutriente fue mayor bajo estrés salino (Fig. 6C). En los frutos de plantas sin estrés salino se incrementó el contenido de Cu con la aplicación de CNT, siendo el tratamiento de 500 mg L^{-1} el que presentó el mayor incremento 108.13% más que el CTRL NS. En los frutos de plantas con estrés salino el contenido de Cu se incrementó con el tratamiento GP a 250 mg L^{-1} en 789.16% en comparación al CTRL NS (Fig. 6D).

El contenido de Zn en las hojas de plantas sin estrés salino no se afectó por los tratamientos de CNMs. En las hojas de las plantas con estrés salino se observó el mayor contenido de Zn con el tratamiento GP a 500 mg L^{-1} , aunque solo fue mayor que el CTRL S en 103.54% (Fig. 6E). En los frutos de las plantas sin estrés salino se incrementó el contenido de Zn con las dosis altas de los dos CNMs, el tratamiento CNT a 500 mg L^{-1} presentó un incremento de 341.93% y el GP a 500 mg L^{-1} 161.75%, en comparación al CTRL NS. Bajo estrés salino el tratamiento CNT a 250 mg L^{-1} disminuyó 28.22% la concentración de Zn en comparación al CTRL S (Fig. 6F).

El contenido de Mn en hojas de plantas sin estrés salino se disminuyó con el tratamiento GP a 500 mg L^{-1} en comparación al CTRL S. En hojas de plantas con estrés salino no hubo

diferencias entre tratamientos; sin embargo, se observó un mayor contenido de Mn bajo estrés salino (Fig. 6G). En los frutos de plantas sin estrés salino se presentó una disminución en el contenido de Mn con los tratamientos de GP a 500 mg L⁻¹ y CNT a 250 mg L⁻¹ en comparación al CTRL NS (31.95% y 33.33%, respectivamente). En los frutos de plantas con estrés salino no se observaron diferencias entre tratamientos (Fig. 6H).

En las hojas de plantas sin estrés salino no se presentaron diferencias entre tratamientos en el contenido de Mo. Bajo condición de estrés salino se observó que el tratamiento GP a 500 mg L⁻¹ presentó la concentración más baja de Mo, aunque no fue significativamente diferente a los controles sonificado y no sonificado (Fig. 6I). En los frutos de plantas sin estrés salino la aplicación de ambos CNMs a 250 y 500 mg L⁻¹ disminuyó la concentración de Mo en comparación al CTRL NS (GP 50-50.74% y CNT 41.04-44.02%). Bajo estrés salino, no hubo diferencias en el contenido de Mo en los frutos (Fig. 6J).

El contenido de B en las hojas de plantas sin estrés salino se incrementó con GP a 250 mg L⁻¹, 26.75% más que el CTRL NS. Bajo estrés salino, solamente se observó una disminución de 25.96% en el contenido de B con CNT a 500 mg L⁻¹ en comparación al CTRL S (Fig. 6K). En los frutos de plantas sin estrés salino se observó una disminución en la concentración de Boro (88.67% con GP y 83.53% con CNT) sobre todo con la dosis alta de ambos CNMs (500 mg L⁻¹), en comparación al CTRL NS. Bajo estrés salino, el tratamiento GP a 250 mg L⁻¹ indujo un incremento de 94.59% en comparación al CTRL NS (Fig. 6L).

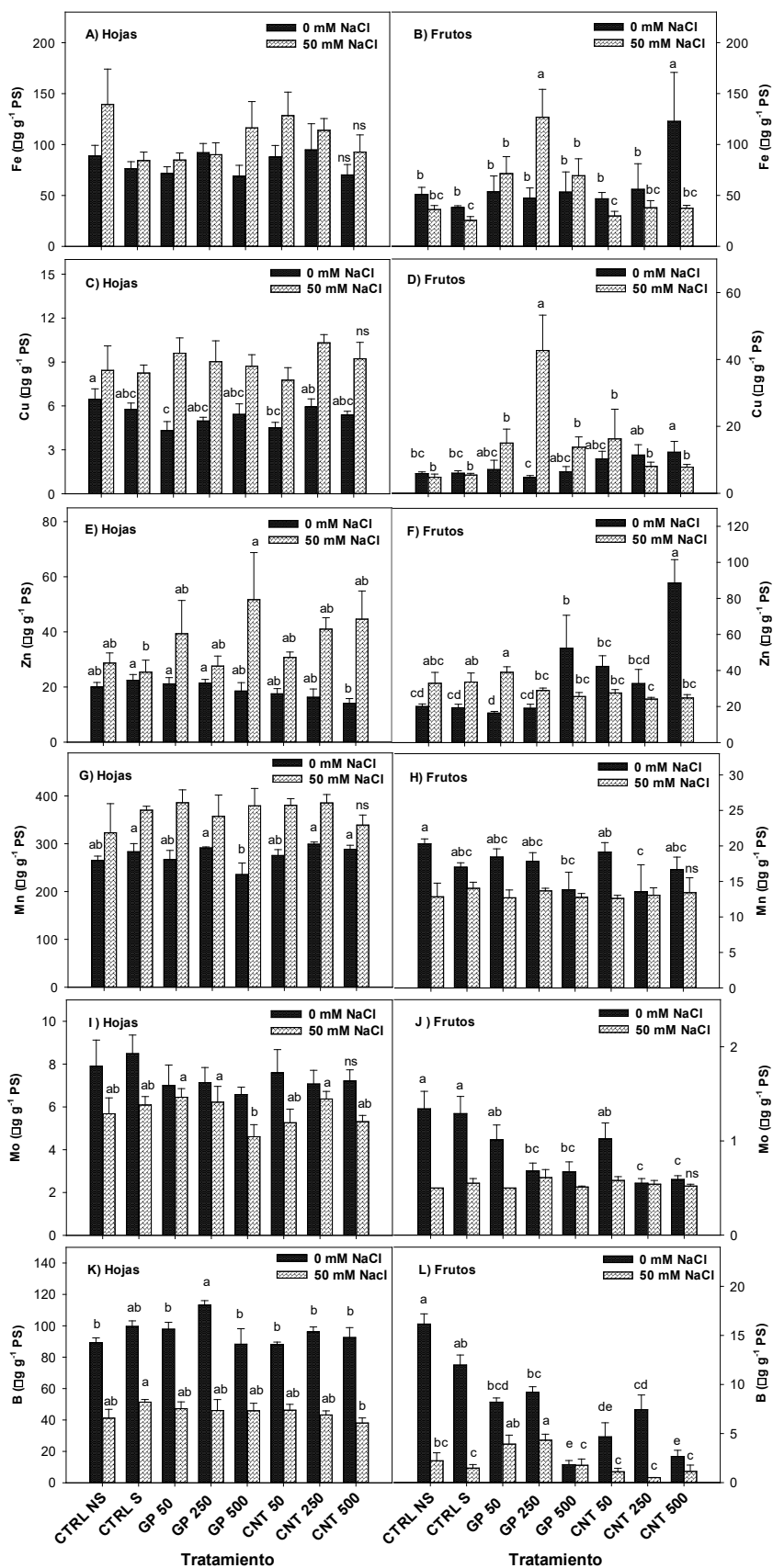


Figura 6. Contenido de micronutrientes en hojas y frutos de las plantas tratadas con CNMs y NaCl. Diferentes letras indican diferencia significativa entre tratamientos de acuerdo a LSD Fisher ($\alpha = 0.05$). ns: no significativo; $n = 6 \pm$ error estándar.

Discusión

Las plantas son un sistema dinámico y flexible capaz de adaptarse a cualquier cambio en su entorno (Arsova et al., 2019). El estrés por salinidad induce cambios morfológicos, fisiológicos y bioquímicos en las plantas, y puede provocar estrés iónico, estrés osmótico y estrés oxidativo, en las plantas (Machado et al., 2020). A su vez, el estrés iónico es causado por la acumulación de iones de sal en las células de la planta por lo que se genera una deficiencia de nutrientes (Hernández, 2019; Hussain et al., 2020). Al respecto, los iones que pueden inducir salinidad son cloruro de sodio (NaCl), sulfato de sodio (Na₂SO₄), sulfato de magnesio (MgSO₄), sulfato de calcio (CaSO₄), cloruro de magnesio (MgCl₂), cloruro de potasio (KCl) y carbonato de sodio (Na₂CO₃), siendo el NaCl la sal más prevalente y de mayor efecto derivado de su disociación en Na⁺ y Cl⁻ (Munns et al., 2019).

Diversos estudios reportan un papel positivo de los CNMs aplicados en plantas. Khodakovskaya et al., (2011) aplicaron CNT (50, 100 y 200 mg L⁻¹) en semillas de tomate cultivadas en medio Murashige y Skoog, y reportaron un incremento en la biomasa de las plántulas y la expresión del gen de las acuaporinas (LeAqp2). Las acuaporinas propician una mayor capacidad de absorción de agua dentro de las semillas y por ende, mayor acumulación de biomasa en las plántulas (Khodakovskaya et al., 2009). Otro gen favorecido por la exposición a los CNT en semillas, es el de las proteínas quinasas, evaluadas en las hojas de tomate, los cuales son un factor importante en el control de la división y el crecimiento celular de las plantas (Khodakovskaya et al., 2013). En el caso del grafeno, Nair et al., (2012) evaluaron el efecto del grafeno (50 mg L⁻¹) en semillas de arroz cultivadas en medio MS (Murashige y Skoog) enriquecido con el nanomaterial, y reportaron efectos positivos sobre las plántulas de arroz, al mejorar la germinación y el crecimiento de raíces y brotes. Mientras que bajo condiciones de estrés salino, se ha demostrado que los CNMs pueden mejorar la capacidad de las plantas para contrarrestar los efectos negativos ocasionados por el estrés. Ballesta et al., (2016), demostraron que la

aplicación de MWCNT ($0-60 \text{ mg L}^{-1}$) en la solución nutritiva Hoagland a plántulas de brócoli, mejoró la germinación y el crecimiento del brócoli (10 mg L^{-1}) bajo estrés salino (100 mM), ya que aumentó la absorción de agua por las raíces y mejoró la asimilación de CO_2 . Además, reportaron mayor acumulación en los niveles de K y Na, seguido de una alta acumulación de MWCNT en plantas bajo estrés de salinidad. Vithanage et al., (2017) menciona que los CNMs pueden adsorber nitrógeno del amoníaco y liberar iones de hidrógeno, lo que mejora la absorción de agua y nutrientes por las plantas. Por lo tanto, se puede esperar una mejoría en la absorción de nutrientes como N, P y K. No obstante, los CNMs pueden transportarse por acción capilar o transpiración, y a medida que la vía de transporte (xilema o floema) se reduce, éstos pueden acumularse y bloquear el paso de nutrientes y otros materiales en la planta, además, una alta concentración de CNMs puede causar aglomeraciones en éstas vías de transporte, lo que ocasiona un desbalance en la absorción de nutrientes y una reducción en el desarrollo y crecimiento de las plantas (Vithanage et al., 2017). Este efecto fue demostrado por Begum et al., (2011), quienes reportaron disminuciones drásticas en la longitud de raíz, tallo y biomasa fresca con las dosis más altas de MWCNT (1000 y 2000 mg L^{-1}) y grafeno ($500-2000 \text{ mg L}^{-1}$) sobre semillas de espinaca roja, lechuga, arroz, pepino, chile y soja. Por lo anterior, se asume que tanto la disminución de los parámetros agronómicos, al igual que la alteración en el contenido de nutrientes observado en este estudio, se debe a una acumulación de CNMs con la dosis más alta en los órganos de las plantas, tratadas en ambas condiciones de estrés.

En general los NMs tienen la capacidad de ingresar al sistema de la planta, a través de las paredes celulares, por la vía del apoplasto, por endocitosis, a través de la absorción de las raíces y translocarse a los diferentes órganos de la planta (Chichiriccò and Poma, 2015; Khodakovskaya et al., 2013; Su et al., 2019b). Sin embargo, en el caso de las semillas la penetración de estos CNMs es más difícil en comparación con otros órganos de las plantas, debido a la cubierta dura de la misma (Khodakovskaya et al., 2009). No obstante, se ha demostrado que al sonicar las semillas se mejora la fluidez de la pared celular al romper la capa rígida creando microporos o microgrietas que facilitan el ingreso tanto de agua como de nutrientes al endospermo de la semilla (Nazari and Etteghadipour, 2017; Rifna et al., 2019). Ratnikova et al., (2015), evaluaron la sonicación de semillas en conjunto con MWCNT (50 mg L^{-1}) en semillas de tomate y reportaron aumentos en la germinación de

semillas, el crecimiento de raíces y biomasa. De acuerdo a los resultados en este estudio, es posible que al sonicar los CNMs junto con las semillas, éstos hayan penetrado a la semilla con mayor facilidad, lo que ocasionó cambios morfológicos en las plantas, debido a que los CNMs pueden actuar como un factor de estrés (Khodakovskaya et al., 2011), activando una cascada de señales para mejorar el sistema de defensa de las plantas y contrarrestar los efectos negativos de posibles estreses bióticos o abióticos (Zhao et al., 2020).

En resumen, existen diferentes respuestas fisiológicas en las plantas expuestas a los CNMs, esto podría deberse a las distintas propiedades de los CNMs, como la forma, tamaño, carga superficial, así como el tiempo de exposición, la vía de aplicación y el cultivo en estudio (Vithanage et al., 2017; Zaytseva and Neumann, 2016). Además, la estructura tubular de los CNT comparado con las láminas de grafeno, puede afectar positiva o negativamente su interacción con el sistema biológico (Zaytseva and Neumann, 2016; Zhang et al., 2015).

Conclusiones

La aplicación de los CNMs muestran resultados diferentes dependiendo de las variables evaluadas así como de las condiciones de estrés del cultivo. Sin estrés salino, el diámetro de tallo y la biomasa seca se incrementaron con los CNMs, mientras que la biomasa fresca disminuyó con CNT (500 mg L⁻¹).

Además, la adición de los CNMs induce efectos tanto positivos como negativos en la absorción de los nutrientes por las plantas. En hojas sin estrés salino, se incrementó el contenido de K, Mg y B, mientras que el S, Cu y Mn disminuyeron. Bajo estrés salino disminuyó el contenido de P, Mo y B; pero se incrementó el contenido de K, Na y Zn. En los frutos sin estrés salino, se redujo el contenido de P, K, Ca, Mg, S, Mn, Mo y B, no obstante, se incrementó el contenido de Fe, Cu y Zn. Bajo estrés salino aumentó el contenido de Mg, Na, Fe, Cu y B, mientras que el Zn disminuyó su contenido.

El Na fue incrementado considerablemente en los órganos de la planta de tomate al estar expuestas a la salinidad, lo que se refleja una reducción del crecimiento y desarrollo de la misma. Sin embargo, se observó que este efecto puede ser contrarrestado al adicionar los

CNMs, al mejorar la altura de la planta, así como la biomasa fresca y seca. Por lo tanto, es de gran importancia conocer las respuestas bioquímicas, metabólicas u otras, que inducen los CNMs en las plantas para entender cómo se da la tolerancia al estrés salino.

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ARTÍCULO 3

Seed priming with carbon nanomaterials impacts in the antioxidant system and biocompounds of tomato plants under saline stress

Seed priming with carbon nanomaterials impacts in the antioxidant system and biocompounds of tomato plants under saline stress

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Abstract

The consumption of food with a high content of bioactive compounds correlate with the prevention of chronic degenerative diseases. Tomato is a food with exceptional nutraceutical value; however, saline stress severely affects the yield and agricultural productivity of this crop. Recent studies have shown that the seed priming can mitigate or alleviate the negative effects caused by this stress. In the present study, the effects of the tomato seed priming with carbon nanotubes (CNT) and graphene (GP) (50, 250 and 500 mg L⁻¹) and two controls (without sonicated and sonicated) were evaluated in the content of photosynthetic pigments in leaves, physicochemical parameters of fruits, as well as enzymatic and non-enzymatic antioxidant compounds, carotenoids and stress signals such as hydrogen peroxide (H₂O₂) and malondialdehyde (MDA) in leaves and fruits of tomato plants without stress saline and with saline stress (50 mM NaCl). The results show that the saline stress in combination with CNT and GP increase the content of chlorophylls,

ascorbic acid, GSH, proteins, and total phenols on the leaves. The addition of CNT and GP increase the activity of enzymes (CAT, APX, GPX and PAL). Likewise, there was also a slight increase in the content of H₂O₂ and MDA in the leaves. Salinity affected the quality of tomato fruits. The physical-chemical parameters and bioactive compounds in tomato with and without saline stress were modified with the addition of CNT and GP. More content of total soluble solids, phenolic compounds, flavonoids, ascorbic acid, lycopene and anthocyanins was observed. The addition of carbon nanomaterials by seed priming in tomato plants subjected to saline stress modify the content of bioactive compounds in tomato fruits, improve the antioxidant defense system of the leaves through enzymatic and non-enzyme compounds, suggesting a possible protection to the plant of negative impacts of stress by salinity.

Keywords: reactive oxygen species, antioxidants, enzymes, graphene, carbon nanotubes, biostimulation, secondary metabolites.

INTRODUCTION

Currently, the main challenges facing global agriculture include climate change, urbanization, environmental problems such as drought, salinity of water and soils, and the accumulation of pesticides and fertilizers (Malik et al., 2021). These problems are further intensified by an alarming increase in the demand for food that will be needed to feed an estimated world population of 9.7 billion by 2050 and 10.9 billion by 2100 (Tommonaro et al., 2021). For this reason, an increase of between 60 and 110% in world food production is required (Godoy et al., 2021). Tomato (*Solanum lycopersicum* L.) is one of the most important horticultural crops in the world due to its high nutritional and economic value (Tommonaro et al., 2021). It is an important source of bioactive compounds such as carotenoids (lycopene and β -carotene), phenolic compounds, and vitamin C, vitamin A and vitamin B (Flores et al., 2021). The consumption of foods with a high content of bioactive compounds is correlated with the prevention of human chronic degenerative diseases, cardiovascular diseases, cancer and neurodegenerative diseases, by reducing the oxidative damage of important biomolecules such as membrane lipids, enzymatic proteins and DNA (Ali et al., 2021).

However, a severe loss in agricultural yield and productivity has been recorded due to saline stress, which affects germination, vegetative growth, fruit formation, development, maturation and fruit quality (Amjad et al., 2019; Vaishnav et al., 2020). Saline stress can cause ionic stress, osmotic stress and oxidative stress in plants, it also alters hormonal homeostasis and causes an imbalance of nutrients (Zulfiqar and Ashraf, 2021). Under conditions of saline stress, it has been shown that there is an increase in ROS (Soltabayeva et al., 2021). A high content of these ROS causes oxidative degradation of biomolecules, such as lipids, proteins, DNA damage, and due to lipid peroxidation that breaks the cell membrane, greater permeability, greater loss of ions and an increase in the MDA content (Godoy et al., 2021).

Plants have several mechanisms to cope with saline stress, these include ROS homeostasis, an increase in the antioxidant defense system, activation of ROS elimination pathways, compartmentalization of toxic ions, osmolyte biosynthesis, as well as an ion homeostasis (Kashyap et al., 2020). To counteract oxidative stress caused by ROS, plants have enzymatic and non-enzymatic detoxification systems, that are more active when plants are under stress (Godoy et al., 2021).

Various strategies have been sought to help plants mitigate the effects of salinity, where the use of nanotechnology stands out, through the application of nanomaterials (NMs) to induce tolerance to salinity in plants (Khan et al., 2017). NMs can be applied in small amounts through different routes (foliar spray, seed, tubers, soil solution or nutrient solution in soilless systems, etc.) to induce greater tolerance to environmental stress and also improve nutraceutical quality of food (Kranjc and Drobne, 2019). NMs have the potential to be used as elicitors for the induction of bioactive compounds in plants, by inducing the expression of genes involved in the biosynthesis of secondary metabolites (Hatami et al., 2019). They also have the ability to mitigate the limitations associated with abiotic and biotic stress, by activating the defense system of plants, through the formation of ROS and the accumulation of bioactive compounds, and triggering other key metabolic activities in stressed plants by salinity (Zulfiqar and Ashraf, 2021). However, the effects of NMs on plants vary, due to the plant species, the growth stage in which they are applied, the method, the duration of exposure, among others, and also depend on the properties

intrinsic characteristics of NMs such as shape, size, chemical composition, concentration, surface structure, aggregation and solubility (Bai et al., 2021). NMs include the use of nanoparticles (NPs) of some metalloids and metal oxides (such as Ag, Cu, Si, Zn, B, Fe and Mn), chitosan, and carbon nanomaterials (CNMs) such as carbon nanotubes (CNTs), graphene (GP) and fullerene. GP is "a two-dimensional crystal composed of mono layers of carbon atoms, arranged in a honeycomb-shaped network", it is the first 2D material available (Carniel et al., 2020). CNTs are unique tubular nanostructures, differing in diameter, length, number of layers, and chirality. Both CNMs produce morphological, physiological and biochemical responses, which help the plant to tolerate some type of stress, whether biotic or abiotic, by generating changes in the transcriptome, proteome, metabolome and ionome (Majumdar and Keller, 2020). The effects of CNMs on plants range from improved seed germination to increased productivity and crop yield (Samadi et al., 2021). At low concentrations they activate the water channel (aquaporins) which improves water absorption, nutrient absorption, seed germination, seedling growth and photosynthesis (Gilbertson et al., 2020). On the contrary, in high doses, CNMs promote the production of free radicals that induce oxidative stress and cell damage. Furthermore, CNMs stimulate the accumulation of bioactive compounds in a dose-dependent manner (Samadi et al., 2021).

Seed priming is a pre-sowing treatment, which places the seeds in a specific, defined solution concentration, for a specified period (Mahakham et al., 2017). Priming stimulates stress responses, through a priming memory in the seeds, activating physiological and metabolic operations, such as DNA repair pathways, de novo protein synthesis, reduction of metabolite leakage, as well as positive regulation in gene expression for the synthesis of antioxidant compounds (Ibrahim, 2016). These responses defend the cell against oxidative damage and lipid peroxidation, and allow to plants to obtain a greater capacity to quickly and effectively combat different types of stress (Rhaman et al., 2021). Shafiq et al. (Shafiq et al., 2021) mention that nano-priming of seeds (soaking of seeds in NMs) is a more efficient and effective process, due to the unique physicochemical properties that NMs possess. Nano-priming triggers special metabolic processes, which are naturally activated and provide protection to seeds during storage, improve germination, growth,

production and quality of crops, and increase the resistance of crops to conditions of abiotic or biotic stress (Malik et al., 2021).

Considering the above, it may be possible that CNMs applied at an optimal dose can act as elicitors and activate the antioxidant defense system to counteract the negative effects caused by saline stress while increasing the production of bioactive compounds. In this context, the priming of tomato seeds with different concentrations of CNMs was carried out in order to evaluate the biochemical responses of tomato plants subjected to saline stress, emphasizing the antioxidant system and bioactive compounds.

MATERIALS AND METHODS

Plant material and carbon nanomaterials

Tomato seeds "Pony Express F1" (Harris Moran, Davis, CA, USA), saladette type and determined growth were used to develop the experiment. The tomato seeds were sterilized in a 2% solution of sodium hypochlorite for 5 min, and rinsed five times with distilled water.

Two carbon allotropes were used: carbon nanotubes (CNTs) and graphene (GP). The CNTs were multilayer (Five layers), approximately 95% pure, 30-50 nm in diameter, and 10-20 μm long (Nanostructured & Amorphous Materials, Inc.). The graphene (GP) was multilayer (10-12 layers), with a purity of 97%, a diameter of 2 μm , and a thickness of 8-12 nm (Cheap Tubes Inc.).

Seed treatment

The treatments consisted of three different concentrations of the two types of carbon nanomaterials: 50, 250 and 500 mg L^{-1} . 40 tomato seeds were immersed in 20 ml of solution with the nanomaterial, and subsequently they were sonicated for 10 minutes in an ultrasonicator (sonicator Q500, QSONICA, Melville, NY, USA) as suggested by Ratnikova et al. (Ratnikova et al., 2015). Additionally, two controls that contained only distilled water were evaluated, one control was the seeds without sonicate (SWS), and the other one were the sonicated seeds (SS). All treatments were stored at room temperature

for 24 hours in their corresponding solutions to allow imbibition with the nanomaterials in the seeds.

Crop development

After 24 hours of imbibition, the treated seeds were sown in polystyrene trays where the seedling developed for 30 days. After this time, the transplant was carried out in black polyethylene bags with a capacity of 14 L. A mixture of perlite-peat moss in a 1:1 ratio was used as substrate.

To evaluate the impact of treatments, two experiments were established, one was developed without any stress condition; and the other the plants were subjected to saline stress from transplantation and throughout the development of the crop (160 days from transplantation). To induce salt stress, 50 mM NaCl always was added to the nutritive solution.

A directed irrigation system was used through which irrigation was applied, and Steiner (Steiner, 1961) nutritive solution was used to provide nutrition to the crop. The pH was adjusted to 6.5 with sulfuric acid each time the nutritive solution was prepared. The electrical conductivity (EC) of the solutions was 1.9-2.5 dS m⁻¹ for the nutritive solution without NaCl, and 5.5-7.5 dS m⁻¹ for the nutritive solution with NaCl.

Physico-chemical analysis of the fruits

For these analyzes, six fruits were selected for each treatment, they were washed with distilled water, and verified that they did not present damage, of uniform size and in a state of maturity 5 (light red) according to the visual color scale of the USDA (United States Department of Agriculture (USDA), 1997). The fruits were collected 70 days after transplantation and from the second cluster, where each fruit was from a different plant. The hydrogen potential (pH), the electrical conductivity (EC), the total soluble solids, the firmness, the oxide reduction potential (ORP), and the titratable acidity were measured as described in Lopez-Vargas et al. (Lopez-Vargas et al., 2018).

Biochemical analysis

Antioxidant compounds and proteins

For this, samples of leaves and fruits were collected at 65 after transplantation, and around noon. The collected leaves were fully developed young leaves, and the fruits presented the same characteristics as those used for the physical-chemical analysis. The samples were collected on ice and stored at a temperature of -20°C . Later they were lyophilized and macerated until obtaining a fine powder.

For the biochemical analyzes, two different extractions were carried out, one to determine hydrophilic compounds as described by Abdel Latef and Tran (Abdel Latef and Tran, 2016), and another to determine lipophilic compounds according to Nagata and Yamashita (Nagata and Yamashita, 1992).

The content of chlorophylls and carotenoids was determined according to Nagata and Yamashita (Nagata and Yamashita, 1992). Vitamin C was made according to Hung and Yen (Hung and Yen, 2002). Reduced glutathione (GSH) was determined by reaction with 5,5 dithio-bis-2 nitro benzoic acid (DTNB) Xue et al. (Xue et al., 2001). The results were expressed in mM GSH EQ 100 g^{-1} DW. The content of total phenols was determined according to Yu and Dahlgren (Yu and Dahlgren, 2000). Total phenols were expressed in mg EQ of Gallic Acid per g^{-1} of DW. The flavonoid content was determined according to Arvouet-Grand et al. (Arvouet-Grand et al., 1994). The results were expressed in mg EQ of quercetin per gram of DW.

The antioxidant capacity was determined by the DPPH (1,1-diphenyl-2-picrylhydrazil) method for both hydrophilic and lipophilic compounds. The total antioxidant capacity was obtained by adding the hydrophilic and lipophilic compounds. The results were expressed as mg EQ of Ascorbic Acid per gram of DW (Brand-Williams et al., 1995). The quantification of proteins was determined using the technique of Bradford (Bradford, 1976) and the results were expressed in mg g^{-1} of DW.

Stress biomarkers

The determination of H_2O_2 was carried out according to the methodology described by Velikova et al. (Velikova et al., 2000), and the results were expressed as $\mu\text{mol g}^{-1}$ of DW. Malondialdehyde (MDA) was determined according to Velikova et al. (Velikova et al., 2000), and the results were expressed as nmol g^{-1} of DW. The determination of ion loss

was carried out according to Jiang and Zhang (Jiang and Zhang, 2001), and the results were presented as % ion loss.

Enzymatic activity

Ascorbate peroxidase (APX) activity (EC 1.11.1.11) was performed according to Nakano and Asada (Nakano and Asada, 1987). The glutathione peroxidase (GPX) activity (EC1.11.1.9) was determined according to Xue et al. (Xue et al., 2001). The catalase activity (CAT) (EC 1.11.1.6) was carried out according to Dhindsa et al. (Dhindsa et al., 1981). Superoxide dismutase (SOD) activity (EC. 1.15.1.1) was performed using the SOD Cayman 706002® kit. The activity of phenylalanine ammonia lyase (PAL) (EC 4.3.1.5) was determined according to Sykłowska-Baranek et al. (Sykłowska-Baranek et al., 2012).

Statistical analysis

The experiment was set up in a completely randomized design and six replicates per treatment were analyzed. The analysis of variance and the Fisher LSD mean comparison test ($\alpha = 0.05$) were performed in the Infostat software (v2020).

RESULTS

Content of photosynthetic pigments in leaves

Without salt stress, the CNT 250 and CNT 500 treatments increased chlorophyll *a* by 17.58% and 23.78% respectively compared to the non-sonicated control. Compared to the sonicated control, the CNT 500 treatment induced an increase of 17.63%. Under saline stress, the GP 500 and CNT 250 treatments increased the chlorophyll content by 8.75% and 13.33% with respect to the non-sonicated control. Compared to the sonicated control, it was observed that the GP in its different doses presented an increase of 9.16-16.81%, and the CNT (50 and 250 mg L⁻¹) an increase of 12.61-21.73% respectively (Fig. 6 A).

Without salt stress, chlorophyll *b* increased only with the CNT 50 treatment by 19.17% compared with the sonicated control. Under saline stress, the GP 500, CNT 50 and CNT 250 treatments increased chlorophyll *b* by 14.57%, 17.01% and 22.89% respectively compared to the non-sonicated control, and 13.11%, 15.52% and 21.33% respectively compared to the sonicated control (Fig. 6 B).

Without salt stress, total chlorophylls increased with the CNT 500 treatment by 19.16% with respect to the non-sonicated control, and 17.32% with respect to the sonicated control. Under saline stress, total chlorophylls increased by 10.57%, 8.65% and 16.32% with GP 500, CNT 50 and CNT 250 respectively with respect to the non-sonicated control (Fig. 6 C).

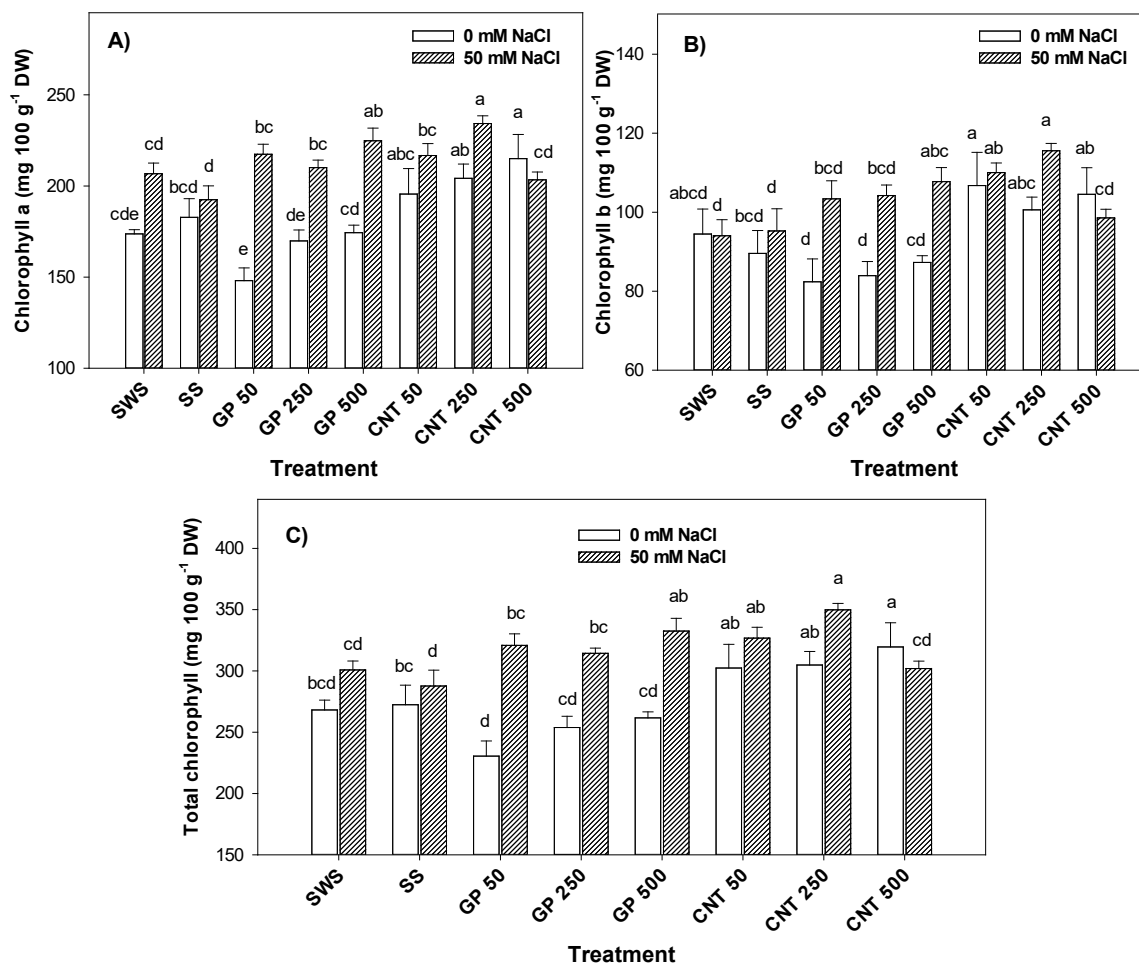


Figure 1. Photosynthetic pigments of tomato leaves treated with carbon nanomaterials and salinity. DW: dry weight; SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). $n = 6 \pm$ standard error.

Stress biomarkers in tomato leaves

The content of hydrogen peroxide (H_2O_2), malondialdehyde (MDA) and the loss of ions (%) in tomato leaves, the results showed significant differences between treatments (Figure 2). Without saline stress, H_2O_2 increased with the addition of CNT in its different doses (50, 250 and 500 mg L^{-1}) being CNT 50 the one with the greatest increase with 52.40% compared to the non-sonicated control, and 41.10% compared to the sonicated control. The GP with the dose of 500 mg L^{-1} increased 22.93% with respect to the non-sonicated control, and 13.81% with respect to the sonicated control. Under saline stress, H_2O_2 increased with GP 500 treatment by 23.50% and CNT 500 by 26.78% with respect to the non-sonicated control, and 17.40% with GP 500 and 20.52% with CNT 500 with respect to the sonicated control (Fig. 2 A).

Without salt stress, the MDA increased with the GP 50 application by 58.91% compared to the non-sonicated control. Regarding the sonicated control, only the GP 250 treatment decreased the MDA content by 20.82%. Under saline stress, the addition of GP 50 increased 41.38% with respect to the non-sonicated control, and 31.08% with respect to the sonicated control; while the addition of CNT 250 mg L^{-1} increased 21.47% with respect to the non-sonicated control (Fig. 2 B).

Without salt stress, the loss of ions decreased by 10.71% with the addition of CNT 500 compared to the non-sonicated control, and compared to the sonicated control it decreased by 13.50%. The GP 500 treatment also decreased the MDA content by 7.10% with respect to the non-sonicated control. Under salt stress, MDA increased by 3.77% when adding CNT 50 and 3.65% with CNT 250. In addition, the sonicated control induced greater ion loss (2.75%) compared to the non-sonicated control (Fig. 2 C).

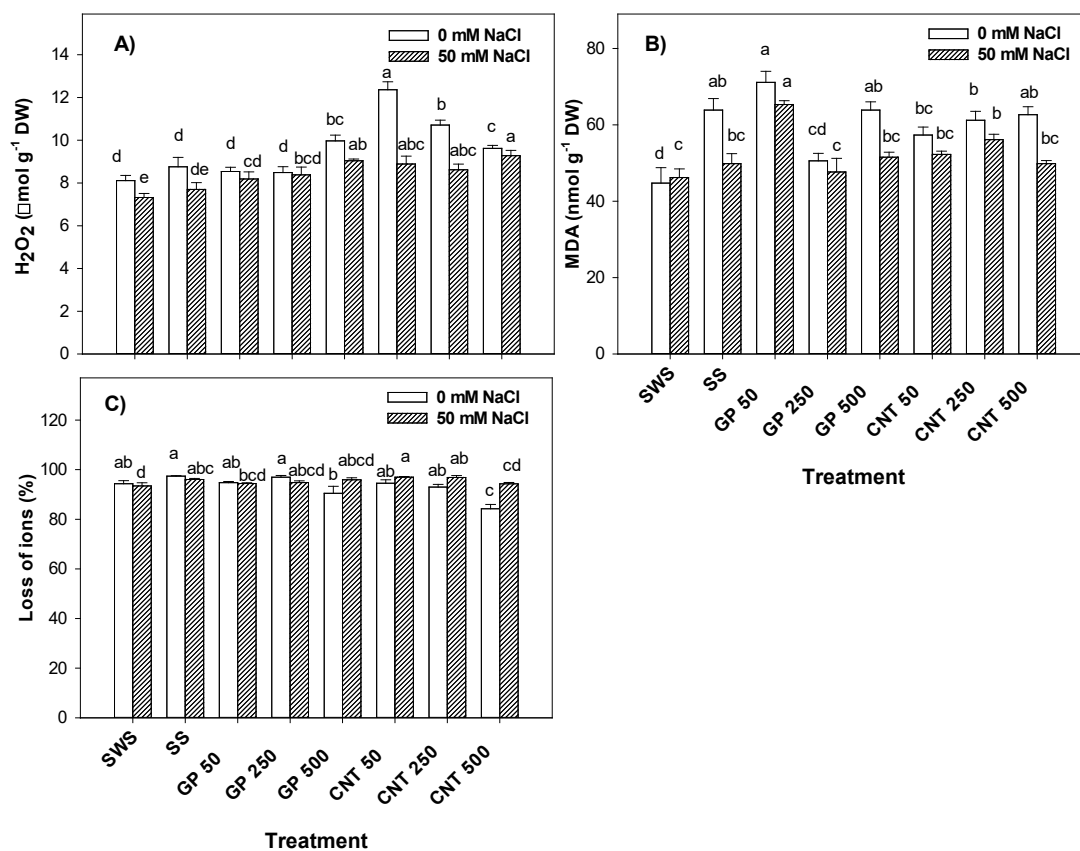


Figure 2. Stress markers in tomato plant leaves treated with carbon nanomaterials and salinity. DW: dry weight; SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). $n = 6 \pm$ standard error.

Proteins and enzymatic activity in leaves

Without salt stress, the protein content increased with the CNT 500 treatment by 22.57% and 14.25% compared to the non-sonicated control and the sonicated control, respectively. In addition, the sonicated control increased the protein content by 7.28% compared to the non-sonicated control. Under salinity conditions, the proteins increased 11.93% with GP 250, 9.91% with CNT 50 and CNT 500 with respect to the non-sonicated control. With respect to the sonicated control, the protein content decreases with the addition of GP 50 (10.78%), GP 500 (4.77%) and CNT 250 (10.00%) (Fig. 3 A).

Without salinity, the activity of GPX increased with the different doses of GP and CNT, where CNT 50 presented the highest value with 114.47% and 35.56% with respect to the

non-sonicated control and sonicated control respectively. Under saline stress, the application of the treatments with GP and CNT decreased the activity of GPX with respect to both controls (Fig. 3 B).

Without salt stress, the addition of CNT 250 increased the APX activity by 51.87% compared to the non-sonicated control. While when comparing the treatments with the sonicated control, the APX activity increased by 140.26% with GP 250 and 56.98% with CNT 250 (Fig. 3 C). Under salt stress, the APX enzyme showed higher activity with CNT 250 with an increase of 24.73% compared to the non-sonicated control. With respect to the sonicated control, all the concentrations of GP and CNT increased the content of APX (Fig. 3 C).

Without salinity, CAT activity increased with the addition of GP in all its doses in a range of 46-97%, while CNT 500 increased it by 28.43%, with respect to the non-sonicated control. Compared to the sonicated control, only GP 500 increases CAT activity by 15.39%. Under salinity, the CNT 50 treatment increased CAT activity by 47.83% compared to the non-sonicated control. While with respect to the sonicated control, the CAT activity decreased significantly with all the treatments (Fig. 3 D).

Without salinity, SOD activity increased with GP 500 by 11.60% and with CNT 500 by 25.00% with respect to the non-sonicated control. Under salinity, the GP 500 and CNT 500 treatments increased SOD activity by 10.54% and 12.58% respectively compared to the sonicated control (Fig. 3 E).

Without salinity, the GP 250 treatment increased PAL activity by 34.75% and 36.13% compared to the non-sonicated control and the sonicated control respectively. Under salinity, PAL activity increased only with CNT 250 by 41.09% with respect to the non-sonicated control (Fig. 3 F).

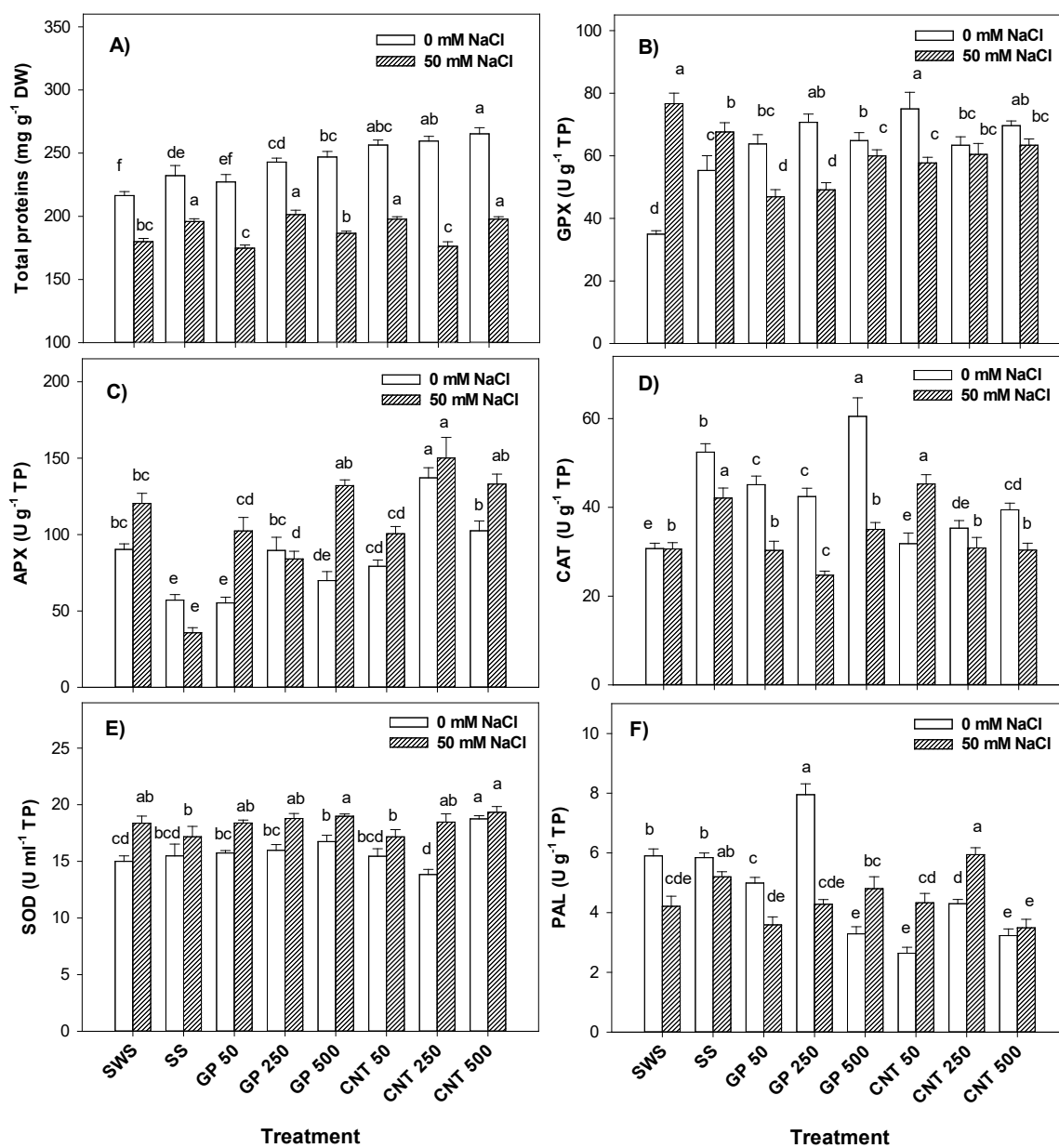


Figure 3. Total proteins and enzymatic activity in tomato leaves treated with carbon nanomaterials and salinity. DW: dry weight; TP: total proteins; SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). $n = 6 \pm$ standard error.

Non-enzymatic antioxidant compounds in leaves

Without salt stress, ascorbic acid decreased with the addition of GP 500 (21.74%) compared to the non-sonicated control. However, with respect to the sonicated control, all treatments increased the content of ascorbic acid in a range of 30.95-47.62%, except for GP 500, which did not show differences. Under saline stress, ascorbic acid increased with the addition of GP 250 by 23.97%, and with all CNT doses in a range of 26-57% with respect to the non-sonicated control. While only the CNT 500 treatment increased the ascorbic acid content by 19.50% with respect to the sonicated control.

Without salinity, GSH increased with GP 250 and CNT 250, by 12.13% and 10.57% with respect to the non-sonicated control, while with respect to the sonicated control the increase was 15.99% and 14.37% respectively. Under salinity, GSH increased with GP 50 (13.62%) and GP 250 (12.53%) with respect to the non-sonicated control, and decreased with GP 500 (13.01%) with respect to the sonicated control. While with CNT 250 an increase of 12.80% was observed with respect to the non-sonicated control, and with respect to the sonicated control it decreased with CNT 500 (11.33%) (Fig. 4 B).

Without salinity, phenols did not show differences between treatments. Under salinity, phenols were increased by the GP 250 treatment in 15.80% with respect to the non-sonicated control, and 14.22% with respect to the sonicated control (Fig. 4 C).

Without salinity, flavonoids decreased by 8.58% with the GP 50 treatment compared to the non-sonicated control, while compared to the sonicated control they increased with GP 250 by 11.56% and with all CNT doses by up to 16.28%. Under salinity, flavonoids decreased compared to the non-sonicated control with GP 50 (9.14%) and with CNT 50 (9.77%). Compared to the sonicated control, the flavonoids content was increased with GP 250 (15.42%) and with CNT 250 (11.98%) (Fig. 4 D).

In antioxidant capacity, differences were observed between treatments. Without salinity, the antioxidant capacity of the hydrophilic compounds increased 8.00% with GP 250 and 10.43% with CNT 500 with respect to the non-sonicated control. Compared to the sonicated control, all treatments induced an increase, being GP 250 and CNT 500 the ones with the greatest increase (12.47% and 15.00% respectively) (Fig. 4 E). Under salinity, the addition of GP (250 and 500 mg L⁻¹) decreased the antioxidant capacity of the

hydrophilic compounds (4.92% and 3.49% respectively) compared to the sonicated control (Fig. 4 E).

Without salinity, the antioxidant capacity of lipophilic compounds increased by 5.63% with CNT 500 with respect to the non-sonicated control, but decreased by 3.91% with GP 50 with respect to the sonicated control. Low salinity, with the exception of GP 500, all treatments induced an increase in the antioxidant capacity of lipophilic compounds compared to the sonicated control in a range of 2.78-4.23% (Fig. 4 F).

Without salinity, the total antioxidant capacity increased with CNT 250 and CNT 500 in 4.36% and 6.90% respectively compared to the non-sonicated control, and CNT 500 increased 6.2% with respect to the sonicated control (Fig. 4 G). Under salinity, the CNT 250 and CNT 500 treatments increased the total antioxidant capacity by 2.92% and 2.47% respectively compared to the sonicated control (Fig. 4 G).

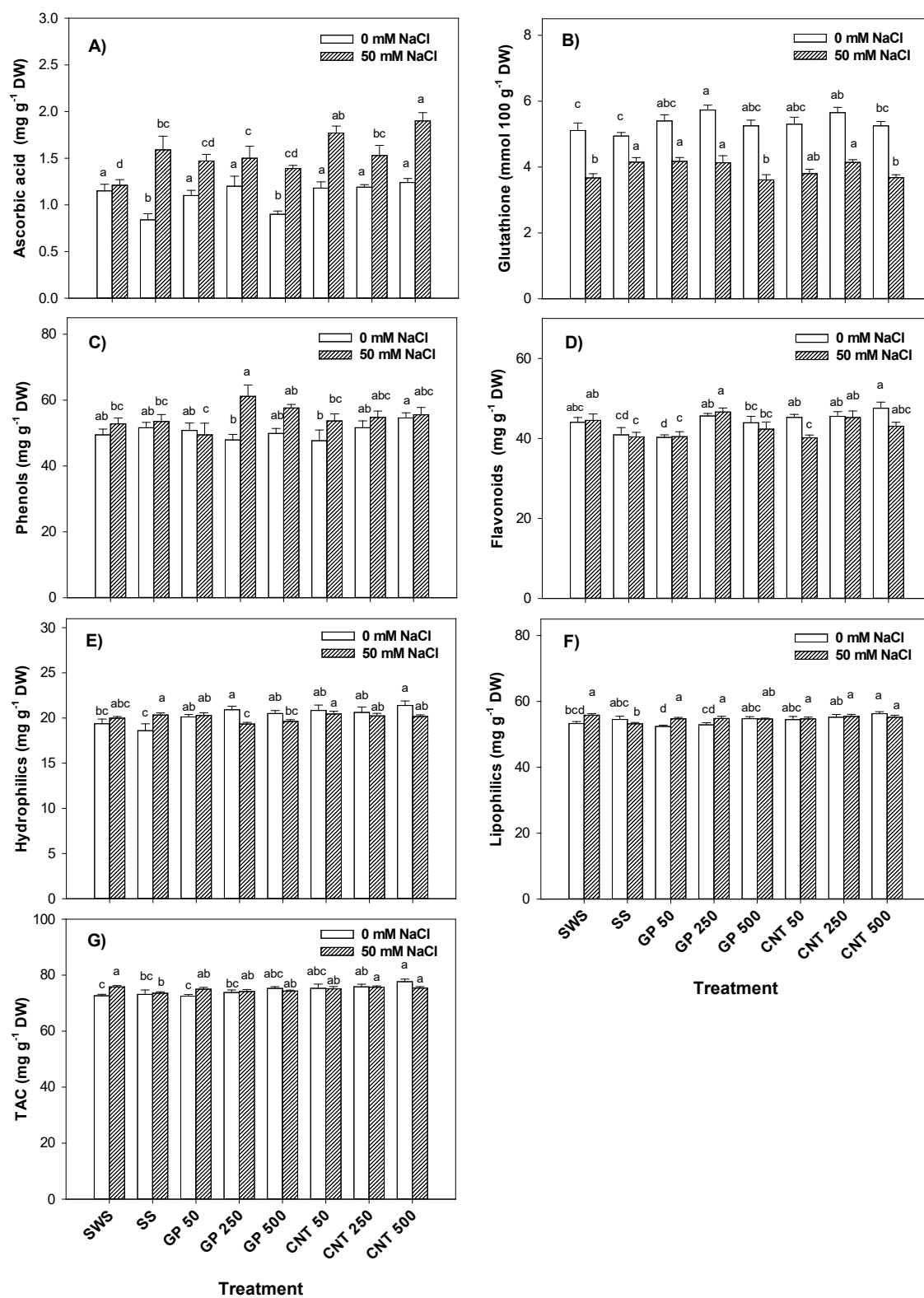


Figure 4. Non-enzymatic antioxidant compounds in tomato plant leaves treated with carbon nanomaterials and salinity. DW: dry weight; TAC: total antioxidant capacity; SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). n = 6 \pm standard error.

Physico-chemical characteristics of the fruits

Without salinity, the firmness of the fruits decreased with the addition of 250 and 500 mg L⁻¹ of GP (10.87% and 13.04%) and CNT (30.43% and 19.57%) compared to the non-sonicated control. Compared to the sonicated control, the doses of 250 and 500 mg L⁻¹ of CNT decreased the firmness of the fruits by 23.81% and 11.90% respectively. Under saline stress, the firmness of the fruits was not affected by the CNMs (Fig. 5A).

Without salinity, the pH of the fruits increased with all the CNT doses by up to 2.26% with respect to the non-sonicated control. Under saline stress, the pH of fruits decreased with CNT 50 by 11.00% and 10.15% compared to the non-sonicated control and the sonicated control respectively (Fig. 5 B).

Without salinity, there were no differences between treatments in the electrical conductivity of the fruits. Under salinity, the EC increased 17.58% with CNT 50 with respect to the non-sonicated control. Compared to the sonicated control, all treatments decreased the EC of the fruits, except CNT 50 (Fig. 5C).

Without salinity, the oxidation-reduction potential in the fruits decreased with all treatments. GP 50 presented the greatest decrease with 52.81% with respect to the non-sonicated control, and 14.94% with respect to the sonicated control. Under salinity, the ORP of the fruits increased with all the doses of GP in a range of 14.03-39.25% with respect to the non-sonicated control. Compared to the sonicated control, only the 50 and 250 mg L⁻¹ doses of GP increased the ORP by 24.22% and 15.96% respectively, while CNT 500 decreased it by 42.81% (Fig. 5D).

Without salinity, the total soluble solids of the fruits increased with the GP 500 (18.42%) and CNT 50 (18.42%) treatments with respect to the non-sonicated control. Under salinity, the TSS of the fruits increased with all the treatments, being GP 500 the one with the highest increase with 25.93% compared to the non-sonicated control (Fig. 5 E).

Without salinity, the titratable acidity of the fruits increased with GP 50 and GP 500 in 13.64% and 36.36% respectively, and with CNT 50 in 29.55%, with respect to the non-sonicated control. Compared to the sonicated control, GP 500 increased TA by 13.21%. Under salinity, the TA of the fruits increased with CNT 50 in 18.18% with respect to the non-sonicated control. Compared to the sonicated control, TA decreased by 19.61% with GP 250, 13.73% with CNT 250 and CNT 500 (Fig. 5 F).

When comparing only the non-sonicated control against the sonicated control in a condition without salinity, a significant difference was observed, the ORP decreased 32.95%, the TSS and the TA increased 15.79% and 20.45%, respectively. And under salinity, an increase was observed in ORP (19.84%), EC (25.42%), TSS (18.52%) and TA (15.91%) in the non-sonicated control. This indicates that the mere fact of carrying out the sonication process induces responses in the physical-chemical quality of the fruits.

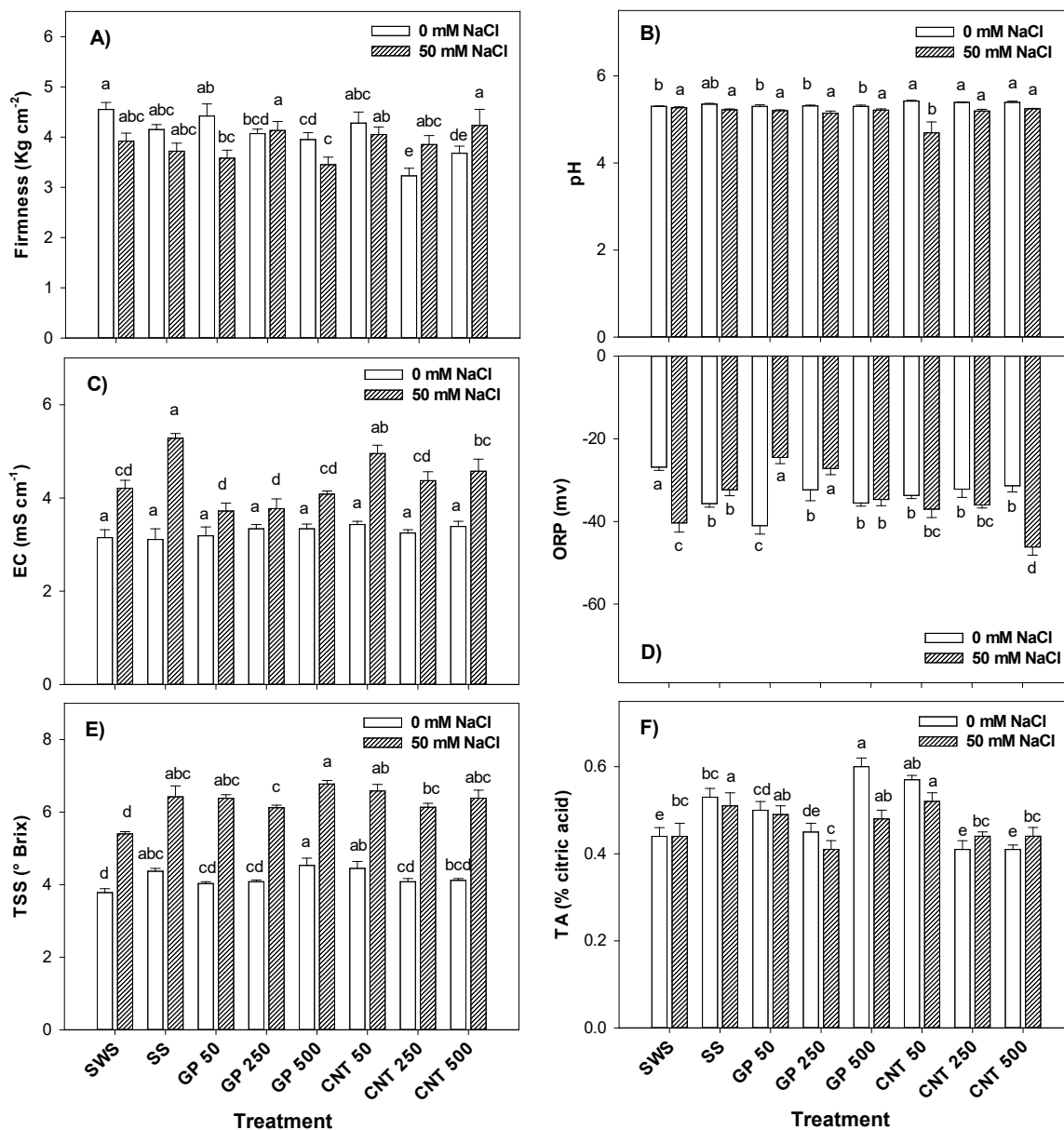


Figure 5. Physico-chemical characteristics of the fruits of tomato plants treated with carbon nanomaterials and salinity. SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). $n = 6 \pm$ standard error.

Bioactive compounds in fruits

Without salt stress, the addition of GP 500 increased the lycopene content by 30.49% with respect to the non-sonicated control. Compared to the sonicated control, the GP 500

increased the lycopene content by 52.33%, while the CNT 250 and CNT 500 treatments increased it by 24.68% and 29.55% respectively. Under salinity, lycopene increased with the GP 50, CNT 50 and CNT 500 treatments by 43.99%, 18.88% and 17.38% respectively compared to the non-sonicated control. Compared to the sonicated control, the GP 50 and CNT 50 treatments increased the lycopene content by 36.25% and 12.49% respectively (Fig. 6 A).

Without salinity, β -carotene increased with the GP 500 and CNT 500 treatments by 10.31% and 26.35% with respect to the sonicated control. Under salinity, the β -carotene content was reduced with CNT 250 by 39.75% compared to the non-sonicated control. In comparison to the sonicated control, there were no differences between treatments (Fig. 6B).

Without salt stress, the GP 500, CNT 50 and CNT 250 treatments decreased the content of ascorbic acid, while the rest of the treatments had no effect. Under saline stress, ascorbic acid was increased with GP 500 and CNT 500 by 28.96% and 27.60% respectively compared to the sonicated control (Fig. 6 C).

Without salinity, GSH increased with all GP and CNT treatments, except GP 250, compared to the sonicated control. Under salinity, GSH increased 10.13% with CNT 50 compared to the non-sonicated control (Fig. 6 D).

Without salinity, phenols increased with CNT 250 (16.11%) and CNT 500 (15.41%) compared to the non-sonicated control. Under salinity phenols increased with CNTs, up to 107.24% with CNT 500 with respect to the non-sonicated control. Compared to the sonicated control, the increase in phenols content was up to 144.85% with CNT 500 (Fig. 6 E).

Without salinity, the flavonoids only decreased with GP 50 with respect to both controls, in the rest of the treatments there were no differences. Under salinity, GP 500 induced a higher content of flavonoids compared to the non-sonicated control (20.48% more), however, the effect was greater with CNTs since all doses increased this variable in a range of 38.94-48.56%. Compared to the sonicated control, only the CNTs increased the flavonoids content up to 37.63% (Fig. 6 F).

Without salinity, the proteins decreased with CNT 250 and CNT 500 in comparison with both controls, the rest of the treatments were the same as the controls. Under salinity, CNT 50 induced 4.65% more proteins compared to the non-sonicated control. Compared to the sonicated control, CNT 50 and CNT 500 increased proteins by 5.29% and 4.45% respectively (Fig. 6 H).

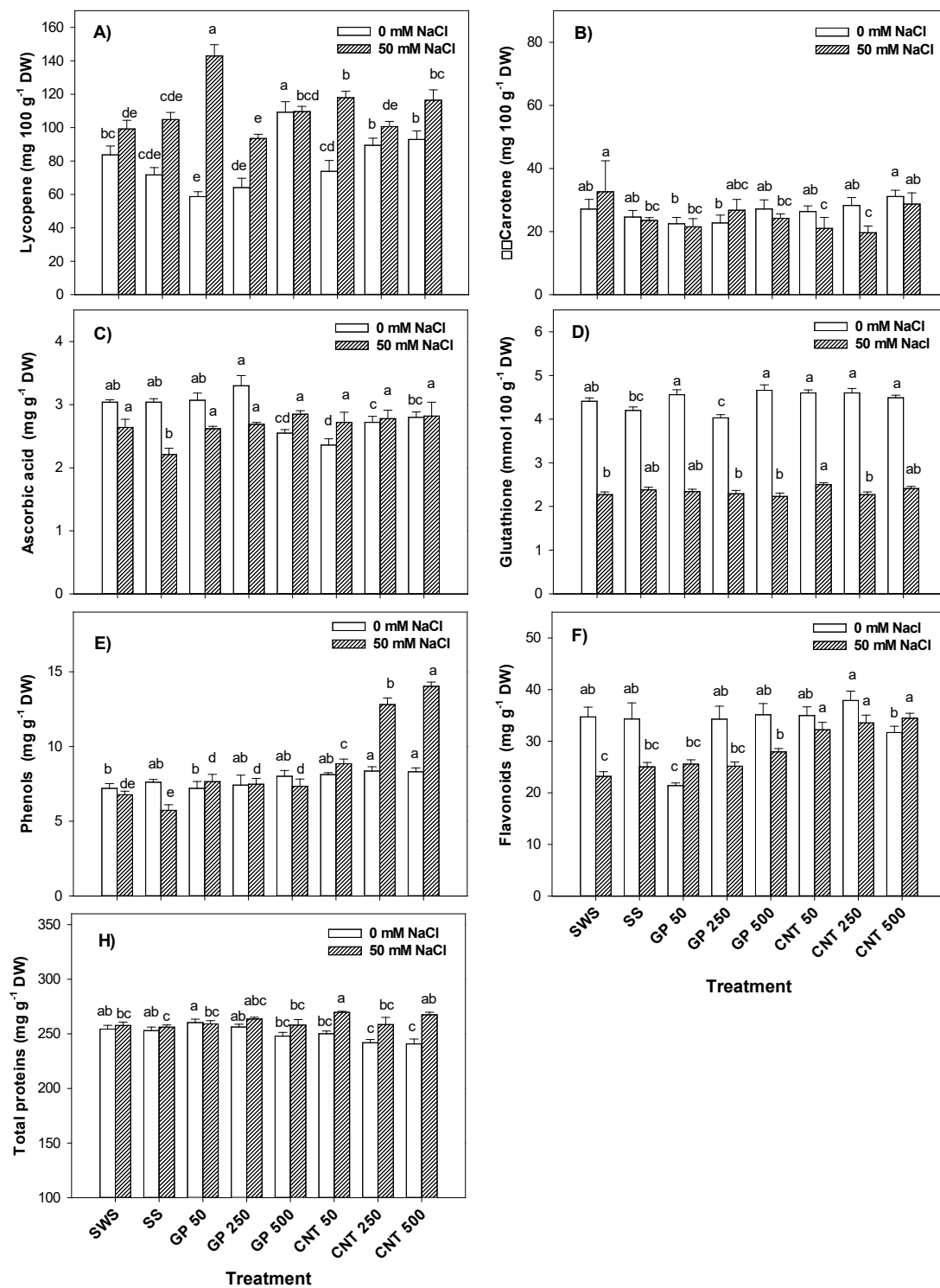


Figure 6. Bioactive compounds in fruits of tomato plants treated with carbon nanomaterials and salinity. DW: dry weight; SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). n = 6 ± standard error.

Antioxidant capacity in fruits

Without salinity, the antioxidant capacity of hydrophilic compounds increased with CNTs in a range of 27.56-55.01% compared to the non-sonicated control. Regarding the sonicated control, they increased 34.04% with CNT 50 and 49.61% with CNT 250. Under salinity, the antioxidant capacity of hydrophilic compounds increased with GP 50 (30.54%), GP 500 (33.97%), CNT 250 (51.81%) and CNT 500 (38.21%) compared to the non-sonicated control. Compared to the sonicated control, it was increased with GP 500 (28.78%), CNT 250 (45.92%) and CNT 500 (32.85%) (Fig. 7 A).

Without salinity, the antioxidant capacity of lipophilic compounds increased with all GP and CNT treatments, except CNT 500, by up to 7.96% with respect to the sonicated control. Under salinity, the different doses of GP increased the antioxidant capacity of lipophilic compounds (15.49-16.50%), however, CNT 500 presented the greatest increase with 56.91% compared to the non-sonicated control. Compared to the sonicated control, CNT 500 presented an increase of 38.43% (Fig. 7 B).

Without salinity, the total antioxidant capacity of the GP treatments had no effect. While the CNT 50 and CNT 500 treatments increased the total antioxidant capacity by 11.57% and 16.45% compared to the non-sonicated control. Compared to the sonicated control, all doses of CNT increased this variable by up to 22.12% with CNT 250. Under salinity, both CNMs presented positive effects. The different doses of GP increased the total antioxidant capacity by up to 22.49% with respect to the non-sonicated control, and 11.45% with respect to the sonicated control. The CNTs increased the total antioxidant capacity by up to 49.94% with respect to the non-sonicated control, and 36.44% with respect to the sonicated control (Fig. 7 C).

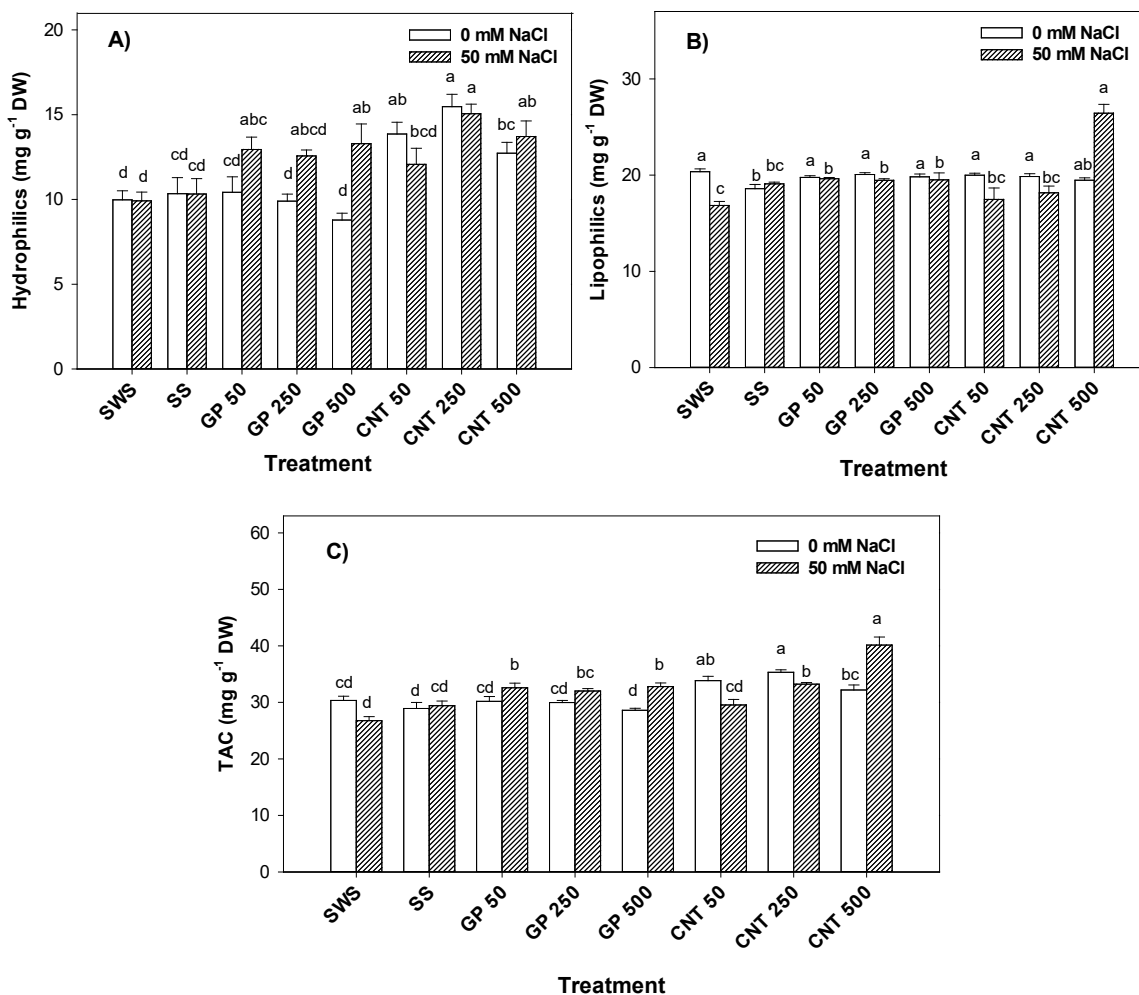


Figure 7. Antioxidant capacity in fruits of tomato plants treated with carbon nanomaterials and salinity. DW: dry weight; TAC: total antioxidant capacity; SWS: seeds without sonicate; SS: sonicated seeds; GP: graphene; CNT: carbon nanotubes; 50, 250 and 500 represent the mg L⁻¹ applied by each carbon nanomaterial. Different letters indicate significant difference between treatments according to Fisher ($\alpha = 0.05$). $n = 6 \pm$ standard error.

DISCUSSION

Saline stress causes a negative impact on several biochemical and physiological processes, due to the increase in the production of ROS or reactive nitrogen species (RNS). Soltabayeva et al. (Soltabayeva et al., 2021) mention that during saline stress, there is an increase in the enzymatic activity of CAT, SOD, APX, GPX, and of bioactive compounds such as ascorbic acid and GSH, among others. In addition, increases in stress markers such as H₂O₂, MDA and loss of ions are also observed during salt stress. H₂O₂ is a signaling

molecule associated with the initiation of stress in plants. Under conditions of saline stress, H_2O_2 acts as a signaling agent causing an ionic balance in plant cells and consequently resistance to it (Latef et al., 2019). However, a high content of H_2O_2 causes an oxidative degradation of biomolecules, due to lipid peroxidation that breaks the cell membrane, causing greater permeability, greater loss of ions and an increase in the content of MDA (Godoy et al., 2021). Increased MDA content is a saline stress response in various crops and is a sign of membrane damage at the cellular level under saline stress (Ibrahim, 2016).

One of the mechanisms of adaptation to stress is the production of antioxidant compounds (which can be bioactive compounds) and a greater activity of the enzymes related to the inactivation of ROS (Abbasi et al., 2016). Antioxidant compounds are biomolecules that prevent the oxidation of other molecules by inhibiting the initiation and elongation of the oxidative chain reaction of ROS (Khan et al., 2017). These compounds are considered the first line of cellular defense used to prevent damage by ROS such as singlet oxygen (1O_2), superoxide anion ($O_2^{\cdot-}$), hydrogen peroxide (H_2O_2) or hydroxyl radicals (OH^{\cdot}) (Sies and Jones, 2020).

The antioxidant defense system of plants includes non-enzymatic compounds, such as ascorbic acid (vitamin C), glutathione, alkaloids, carotenoids (lycopene and β -carotene), flavonoids, phenolic compounds and tocopherols (Fabián Pérez-Labrada et al., 2019). While the enzymatic compounds include enzymes like SOD, CAT, APX, GPX, mono dehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), glutathione reductase (GR), glutathione transferase (GST), guaiacol peroxidases (POX) and similar proteins to nicotinamide adenine dinucleotide phosphate (NADPH), among others (Choudhury et al., 2013). All this defense machinery of plants are more active when they are subjected to stress (Godoy et al., 2021). Under conditions of saline stress, it has been shown that there is an increase in ROS (Soltabayeva et al., 2021). The SOD enzyme is the initial line of defense as it catalyzes the dismutation of the superoxide radical ($O_2^{\cdot-}$) to hydrogen peroxide (H_2O_2) and molecular oxygen (O_2). The enzymes APX, GPX and CAT participate in the transformation of H_2O_2 into H_2O and oxygen. APX requires ascorbic acid and reduced glutathione as substrates, while GPX uses GSH as a reducing agent. CAT is highly specific for H_2O_2 and does not require an activity reducer. An

increase in the enzymatic activity of CAT effectively eliminates ROS produced during salt stress (mainly in the peroxisome) in plants (Vaishnav et al., 2020). While the PAL enzyme catalyzes L-phenylalanine to transcinamic acid to produce secondary metabolites, such as lignin, flavonoids and other compounds, products of the phenylpropanoid pathway, which can also be antioxidants (Younes et al., 2019).

The NMs applied in seeds, enter through the parenchymal intercellular spaces of the cover, until they reach the cotyledon. Once inside, the absorption of NMs in the cotyledons is regulated by aquaporins (Khodakovskaya et al., 2009, 2011). However, the hard coating of the seeds does not ensure the penetration of the NMs into the interior of the seed. As an alternative, some authors propose the sonication of seeds, since it has been shown that this process improves the fluidity of the cell wall by creating micropores or microcracks, which facilitate the entry of both water and nutrients to the endosperm of the seed (Rifna et al., 2019). In addition, it has been reported that by sonicating the seeds together with the CNMs, not only the entry of the CNMs is facilitated, but the dispersion of the nanomaterial is also improved, which avoids agglomerations (Ratnikova et al., 2015).

It has been reported that through imbibition, some NMs, such as CNTs, can break down the hard layer of the seed and create pores to enter the seed (Khodakovskaya et al., 2009; Ratnikova et al., 2015). The priming of seeds with NMs activates a series of physiological and metabolic responses, such as an increase in gene expression to synthesize bioactive compounds, and enzymatic antioxidant compounds that regulate ROS homeostasis (Ibrahim, 2016). These responses increase the antioxidant system of plants, which allows a greater capacity to mitigate the negative effects of any stress and induce tolerance (Rhaman et al., 2021). In general, nano-priming of seeds increases the resistance of crops to abiotic or biotic stress conditions (Malik et al., 2021).

NMs have the potential to be used as elicitors or biostimulants for the induction of bioactive compounds in plants, since they positively modify the expression of genes involved in the biosynthesis of secondary metabolites (Samadi et al., 2021). These metabolites are also capable of mitigating the limitations associated with saline stress (Zulfiqar and Ashraf, 2021). At low concentrations, NMs activate the aquaporin channel and promote water and nutrient absorption (Gilbertson et al., 2020), while in high doses,

NMs promote the production of free radicals that induce oxidative stress and cell damage (Samadi et al., 2021). Therefore, it is of utmost importance to define the appropriate doses to achieve the desired effect on the plants, and to avoid possible negative impacts.

Some authors mention that the responses of plants exposed to abiotic stresses, combined with some biostimulant, are different from those observed when applied separately. The combination of elicitors can be synergistic or antagonistic and, consequently, it translates into a relief or a total failure of the plants to survive under biotic or abiotic stresses (Amjad et al., 2019).

Several authors have reported the use of CNMs in seed priming and in the induction of tolerance to environmental stresses. Hatami et al. (Hatami et al., 2017) exposed *Hyoscyamus niger* L. seeds with single-walled CNTs (SWCNT) ($50\text{-}800\ \mu\text{g ml}^{-1}$) under different levels of drought stress ($0.5\text{-}1.5\ \text{MPa}$). The results showed that with low concentrations of SWCNT tolerance can be induced in seedlings against low levels of drought by improving water absorption and activating the plant defense system (SOD, POD, CAT and APX) as well as the biosynthesis of proteins, phenolics and specific metabolites such as proline. A reduction in oxidative damage indices, including H_2O_2 , malondialdehyde content, and electrolyte leakage was also observed. Abdel Latef et al. (Latef et al., 2017), evaluated the priming of lupine plant seeds (*Lupinus termis* L.) with different concentrations of ZnO NPs (20, 40 and $60\ \text{mg L}^{-1}$) and exposed to NaCl ($150\ \text{mM}$). Salinity stress increased the content of organic solutes (soluble sugar, soluble protein, total free amino acids and proline), total phenols, MDA, ascorbic acid and Na, as well as the activities of SOD, peroxidase (POD) and APX in plants stressed on control plants. Shafiq et al. (Shafiq et al., 2021), investigated the effects of priming wheat seeds with fullereneol (0, 10, 40, 80 and $120\ \text{mg L}^{-1}$) under saline stress ($150\ \text{mM NaCl}$). The results showed an increase in enzymatic activities, a reduction in the content of photosynthetic pigments (chlorophyll a and b, and carotenoids) and an alteration in ion absorption.

Fan et al. (Fan et al., 2018) reported that multiple-walled CNTs (MWCNTs) positively affect the photosynthesis system of plants by stimulating the electron transport rate and the photochemical quantum yield of photosystem II up to 12% compared to the control.

CNTs improve the functioning of photosynthetic machinery because they can be integrated into the outer lipid envelope of chloroplasts; its semiconductor capacity triples photosynthetic activity through increased electron transport (Giraldo et al. 2014). Giraldo et al. (2014), explain that chloroplasts exposed to SWCNT stimulate photosynthetic activity and increase electron transport flux by increasing photo-absorption by chlorophylls. Baz et al. (Baz et al., 2020), evaluated the priming of lettuce seeds (*Lactuca sativa* L.) with carbon nanoparticles (CNP) soluble in water (0.3%) and under saline stress (150 mM NaCl). The pretreatment with CNP promoted the accumulation of the total chlorophyll content of the seedlings grown under saline stress. Joshi et al. (Joshi et al., 2018b) applied MWCNT (90 $\mu\text{g ml}^{-1}$) in oats by means of the seed priming method and reported an increase in the chlorophyll content (57%), while the photosynthetic activity increased by 15% and therefore obtained a better performance. Joshi et al. (Joshi et al., 2020) used MWCNT (70, 80 and 90 $\mu\text{g ml}^{-1}$) to prime rice seeds. As a result, it was observed that the plants treated with MWCNT had denser stomata and longer roots, which resulted in a faster growth and facilitated the absorption of water and minerals, thus increasing the crop yield. In addition, the chlorophyll content and photosynthetic activity were improved. Gohari et al. (Gohari et al., 2020) evaluated COOH-functionalized MWCNTs (MWCNTs-COOH) (0, 25, 50 and 100 mg L^{-1}) in sweet basil (*Ocimum basilicum* L.) seedlings under saline stress (50 and 100 mM NaCl). The results showed that the application of MWCNTs-COOH at an optimal concentration (50 mg L^{-1}) can improve the negative effects of salinity stress by increasing the content of chlorophylls and carotenoids and inducing enzymatic antioxidant components such as APX, CAT and guaiacol peroxidase, and non-enzymatic like phenols. Zhao et al. (Zhao et al., 2015), mentions that 1000 $\mu\text{g L}^{-1}$ of graphene oxide (GO) in *Arabidopsis thaliana* seedlings under saline stress (200 mM) increased H_2O_2 . Salinity induced a higher generation of ROS (48.1% $\text{O}_2^{\cdot-}$ and 62.2% H_2O_2) and lipid peroxidation (40.8% MDA).

Park and Ahn (Park and Ahn, 2016) reported a decrease in the total protein content in carrot seeds when evaluating CNTs (0-2000 mg L^{-1}) for 5 days. Both authors mention that cultures with low protein levels could be more sensitive to some type of stress, in addition to the fact that their expression or stability depends on the tissue or stage of development of the culture under study.

Fruit quality parameters for tomatoes include sugar content, pH, electrical conductivity, titratable acidity and reducing sugar content, as well as firmness determine freshness and storage stability (Ali et al., 2021). Saline stress (≥ 4 dS m^{-1}) affects the formation, development, maturation and quality of tomato fruits (Amjad et al., 2019), causes osmotic stress, an active accumulation of solutes (Moya et al., 2017), and breaks ion homeostasis (Basu et al., 2020). A variation in the levels of K^+ , modifies the levels of organic acids (citric and malic) in tomato fruits (Gruda et al., 2018). While low levels of Ca^{2+} caused by the low translocation of Ca^{2+} towards the fruits negatively affect the firmness of the fruit and, consequently, the shelf life, due to the low content of calcium pectates in its middle sheet (Martínez-Damián et al., 2018).

The EC of the fruits can be increased by saline stress due to a reduction in the size of the fruits, a low accumulation of water and a higher content of solutes (Rodríguez-Ortega et al., 2019). The increase in pH values in tomato fruits can be attributed to the imbalance between K^+/Na^+ and SO_4^{2-}/Cl^- ions, which maintain the stability of the pH of tomato fruits (Anthon et al., 2011). A decrease in the ORP indicates a better quality of the fruit, since it can translate into a greater antioxidant potential (Juarez-Maldonado et al., 2016). Titratable acidity is a parameter that decreases in parallel with the evolution of fruit maturity, since organic acids are used as a substrate in the respiration process. The priming of seeds with CNMs and the saline stress modified the quality parameters in tomato fruits. Morales-Díaz et al. (Morales-Díaz et al., 2017) mention that when plants are subjected to abiotic stresses, it is possible that the presence of NPs and NMs interacts synergistically or antagonistically causing adverse responses in plants.

CONCLUSIONS

The use of CNMs in the nano-priming of tomato seeds has a positive impact on the accumulation of proteins and antioxidant compounds in the leaves. However, this effect was more evident under NaCl stress, since the combination of CNMs + NaCl potentiated the increase of enzymatic and non-enzymatic antioxidant compounds.

The increase in antioxidant compounds seems to be consistent since the use of CNMs improved the antioxidant capacity of the fruits, by increasing lycopene, glutathione. While

the combination of CNMs and salt stress increased lycopene, ascorbic acid, phenols, glutathione and flavonoids.

CNMs can be used as eliciting agents in seed nano-priming, to improve the antioxidant system of plants and the quality of tomato fruits. However, it is necessary to define the optimal treatments in terms of CNMs used and concentration to obtain the desired positive effects. Furthermore, the use of CNMs in nano-priming is not applied directly to the soil, so the dispersion of large amounts of NMs in ecosystems can be avoided.

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CONCLUSIONES GENERALES

La preparación de semillas con CNMs no afectó la germinación de las plantas de tomate. Solo las dosis altas indujeron un efecto negativo. Sin embargo, los CNMs afectaron negativamente la longitud de la raíz y el peso fresco del hipocótilo, y promovieron el crecimiento de la raíz. La preparación de semillas con CNMs indujo cambios significativos en el crecimiento de las plántulas de una manera dependiente de la concentración. El vigor de las plántulas de tomate se promovió generalmente con grafeno y CNT en dosis bajas. Sin embargo, las altas dosis de ambos CNMs tuvieron efectos negativos. Por tanto, es importante considerar las concentraciones utilizadas para obtener resultados favorables en el crecimiento de las plántulas.

El cebado de semillas con grafeno favoreció el aumento de clorofilas, así como el contenido de proteínas y antioxidantes no enzimáticos (vitamina C, β -caroteno, glutatión, fenoles y flavonoides) de las plántulas de tomate. Sin embargo, la capacidad antioxidante fue mayor con el uso de CNT para la preparación de semillas. Asimismo, ambos CNMs promovieron la actividad enzimática; los CNT aumentaron las enzimas PAL, APX y CAT, mientras que GPX y SOD fueron mayores con el grafeno. Por tanto, el cebado de semillas con CNMs tuvo efectos pronunciados sobre el sistema antioxidante de las plantas de tomate, presentando diferentes respuestas según el tipo de CNMs empleado.

La preparación de semillas con nanomateriales de carbono indujo respuestas favorables que podrían mejorar potencialmente el desarrollo del cultivo de tomate. Estos resultados indicaron que el tratamiento de semillas de tomate con nanomateriales de carbono podría ser una buena opción para inducir la bioestimulación, además de demostrar un método fácil de aplicación.

La aplicación de los CNMs mostraron resultados diferentes dependiendo de las variables evaluadas y las condiciones de estrés del cultivo. Sin estrés salino, el diámetro de tallo y la biomasa seca se incrementaron con los CNMs, mientras que la biomasa fresca disminuyó con CNT (500 mg L⁻¹).

Además, la adición de GP y CNT indujo efectos positivos y negativos en la absorción de los nutrientes por las plantas. Sin estrés salino se incrementó el contenido de K, Mg y B en las hojas, mientras que el S, Cu y Mn fueron disminuidos. Bajo estrés salino disminuyó

el P, Mo y B; pero se incrementó el K, Na y Zn. En los frutos, sin estrés salino se redujo el contenido de P, K, Ca, Mg, S, Mn, Mo y B, no obstante, se incrementó el contenido de Fe, Cu y Zn. En los frutos bajo estrés salino aumentó el contenido de Mg, Na, Fe, Cu y B y disminuyó el Zn.

El contenido de Na se incrementó considerablemente en los órganos de la planta al estar expuestas a la salinidad, lo que se asoció con una reducción en el crecimiento y desarrollo de la misma. Sin embargo, se observó que este efecto fue contrarrestado al adicionar GP y CNT, logrando mejorar la altura de la planta y la biomasa fresca y seca. Por lo tanto, es de gran interés conocer las respuestas bioquímicas que inducen los CNMs en las plantas para entender mejor la tolerancia al estrés salino.

El uso de CNMs en el cebado de semillas de tomate tuvo un impacto positivo en la acumulación de proteínas y compuestos antioxidantes en las hojas. Sin embargo, este efecto fue más evidente bajo estrés por NaCl, ya que la combinación de CNMs + NaCl aumentó los compuestos antioxidantes enzimáticos y no enzimáticos.

El aumento de compuestos antioxidantes fue constante ya que el uso de CNMs mejoró la capacidad antioxidante de los frutos, al incrementar el licopeno y el glutatión. Mientras que la combinación de CNMs y estrés salino aumentó el licopeno, el ácido ascórbico, los fenoles, el glutatión y los flavonoides.

Los CNMs se pueden utilizar como agentes estimulantes en el cebado de semillas, para mejorar el sistema antioxidante de las plantas y la calidad de los frutos del tomate. Además, el uso de CNMs en nanocebados evita la aplicación al suelo, por lo que se disminuye la dispersión de NMs en los ecosistemas. Sin embargo, para lo anterior es necesario definir los tratamientos adecuados en términos de CNMs utilizados y concentración para obtener los efectos positivos deseados. Además, cabe resaltar que la sonicación de las semillas presenta efectos beneficios y adversos comparado con las semillas sin sonicar, por lo que también es necesario considerar este pre-tratamiento como un factor que podría generar sinergismo o antagonismo al combinarlo con CNMs.

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