

Revisión bibliográfica

## **Toxicidad del Cadmio en las plantas y estrategias para disminuir sus efectos. Estudio de caso: El tomate**

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### **RESUMEN**

El cadmio (Cd) es uno de los metales pesados más tóxico. Su alta movilidad y poder bioacumulativo lo diferencian del resto de los de su grupo y motivan el interés de los científicos por conocer sus efectos e interacción con las plantas. En el presente trabajo, se realizó una revisión bibliográfica de los principales mecanismos de entrada y transporte del Cd en las plantas y sus efectos tóxicos en las mismas. También, se abordan temas como, los mecanismos de defensa de las plantas ante el estrés por Cd y las estrategias existentes para disminuir su toxicidad. Dentro de los diferentes cultivos, el tomate resulta de especial interés,

debido a que es la hortaliza más difundida en el mundo y ha mostrado ser una planta tolerante al Cd y con potencialidades para su acumulación.

**Palabras clave:** metales pesados, relación, hortalizas

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## INTRODUCCIÓN

El cadmio es un metal de transición altamente tóxico a niveles de exposición muy bajos y tiene efectos agudos y crónicos sobre la salud de las plantas, animales, seres humanos y todos los seres vivos en general. Como consecuencia de la actividad industrial y la antropización, se estima que 30,000 toneladas de Cd son liberadas al medio ambiente cada año <sup>(1)</sup>. Por tanto, en diferentes lugares del planeta y en nuestro país se han detectado niveles de Cd en agua, suelo y plantas que superan los límites permisibles establecidos para diferentes usos <sup>(2-7)</sup>.

El cadmio no es degradable en la naturaleza, por lo que una vez liberado al medio ambiente, permanecerá en circulación. Esta propiedad unida a su alta movilidad, poder bioacumulativo y toxicidad a concentraciones muy bajas lo convierten en uno de los metales pesados de mayor importancia. En la década de los años 60, la contaminación ambiental con este metal se puso de manifiesto cuando en Japón más de 100 personas murieron por una enfermedad que se nombró Itai-Itai, la cual estaba ocasionada por altas concentraciones de Cd en el río Jinzu, en el arroz ( $4,2 \text{ mg L}^{-1}$ ) y consecuentemente en el cuerpo humano <sup>(8)</sup>. Estos hechos motivaron el interés de la ciencia del suelo y las plantas por conocer y controlar los efectos que el metal producía en diferentes cultivos.

Se reconoce este metal como uno de los más tóxicos e inhibitorios de los procesos fisiológicos de las plantas. Estudios en varios cultivos han evidenciado que reduce el crecimiento, la actividad fotosintética, la transpiración y el contenido de clorofilas <sup>(9-12)</sup>. También, provoca clorosis, estrés oxidativo, desequilibrios nutricionales y modifica la actividad de enzimas, involucradas en el metabolismo de los ácidos orgánicos y en el ciclo de Krebs <sup>(13-16)</sup>. De manera general, las afectaciones provocadas en algunos procesos fisiológicos, pueden ser tan marcadas que las plantas no son capaces de evadirlas y se manifiestan en otros procesos. La toxicidad por Cd puede llevar a la muerte de la planta y

ello depende, entre otros factores, del tiempo de exposición, el contenido del metal y las adaptaciones específicas que desarrollan.

Las adaptaciones específicas de las plantas al estrés por Cd se basan en dos mecanismos principales; algunas evitan o regulan la entrada y transporte del mismo <sup>(2,17)</sup> y otras toleran determinados contenidos de Cd, a través de su detoxificación, mediante quelación en orgánulos intracelulares <sup>(18)</sup>. Basándose en estos mecanismos de tolerancia, varios grupos de investigación han propuesto diferentes estrategias para aminorar los efectos del Cd en las plantas. La mayoría de las estrategias incluyen realizar modificaciones en el manejo de la nutrición <sup>(19)</sup>. Pero otras prácticas también han mostrado resultados favorecedores, tales como, la inoculación con bacterias beneficiosas <sup>(3,20)</sup>, injertos sobre patrones resistentes <sup>(21,22)</sup>, adición de diferentes reguladores del crecimiento <sup>(23,24)</sup> y aplicación de enmienda en el suelo. Conocer la interacción del Cd con las plantas, así como la búsqueda de alternativas para minimizar sus efectos ha atrapado el interés de la comunidad científica, producto del crecimiento acelerado de la contaminación con este metal y su alta toxicidad. El objetivo del presente estudio es hacer una revisión actualizada sobre resultados de investigaciones relacionadas con estos aspectos.

Dentro de los diferentes cultivos, el tomate resulta de especial interés, debido a que es la hortaliza más difundida en el mundo y de mayor valor económico. Se ha utilizado no solo como alimento, sino también como planta modelo en disímiles investigaciones. La planta de tomate tiene muchas características interesantes, como la fruta carnosa, un brote simpodial y hojas compuestas, que otras plantas modelo (por ejemplo, el arroz y la Arabidopsis) no tienen <sup>(25)</sup>. Además, algunas de sus variedades han mostrado ser una planta tolerante al Cd, con potencialidades para su acumulación <sup>(26)</sup>.

### **Absorción y transporte del cadmio en las plantas**

El Cd entra a la planta principalmente en forma de Cd<sup>2+</sup>, ya que sus iones quelatos, generalmente, no están disponibles para la absorción por las raíces. La capa de células epidérmicas es el primer tejido para la captación de iones y dentro de ella, los pelos radicales son la zona más activa para absorber iones del suelo y es la estructura que facilita la absorción de Cd<sup>2+</sup> <sup>(27)</sup>

Se han propuestos tres diferentes vías de entrada de Cd en la raíz <sup>(28)</sup>:

*Primera vía:* en la membrana plasmática de las células epidérmicas de la raíz, el  $\text{CO}_2$  (ac) se disocia en  $\text{H}^+$  y  $\text{HCO}_3^-$ , a través de la respiración de la planta. El  $\text{H}^+$  se intercambia con el  $\text{Cd}^{2+}$  del suelo y el metal se adsorbe en la superficie de las células epidérmicas de la raíz. Este proceso de adsorción es rápido y no requiere de energía y es la etapa precedente a la posterior absorción de  $\text{Cd}^{2+}$  en la epidermis a través de la vía del apoplasto.

*Segunda vía:* el Cd es un elemento no esencial y, por tanto, se asume que las plantas no disponen de mecanismos de entrada específicos para él. Ingresa a las células vegetales a través de los transportadores de metales esenciales  $\text{Fe}^{2+}$ ,  $\text{Zn}^{2+}$  y  $\text{Ca}^{2+}$ , como es el caso de las proteínas IRT1 y LCT1. Después de combinado con las proteínas transportadoras, el Cd entra en la capa de epidermis de la raíz, a través de la vía del simplasto.

*Tercera vía:* para aumentar la disponibilidad de iones en el suelo de la rizosfera, las raíces de las plantas secretan compuestos de baja masa molecular, como los ácidos mugineicos (MA), que forman complejos con el  $\text{Cd}^{2+}$ . Por tanto, el  $\text{Cd}^{2+}$  ingresa a la capa de la epidermis de la raíz a través de las proteínas tipo YSL en forma de quelatos.

El movimiento de Cd desde la raíz hacia el tallo se controla a través de tres procesos: el secuestro de metales dentro de las células de la raíz; el transporte hacia la estela y la liberación del metal al xilema <sup>(29)</sup>. La retención es producto de las barreras apoplásticas y la quelación en vacuolas, se demostró que las fitoquelatinas y otros tioles son los quelantes principales en el secuestro de Cd en la raíz <sup>(30)</sup>. Otro de los mecanismos propuestos de retención del Cd en raíces es a través de la impregnación de la suberina en la pared celular durante la maduración de exodermis y endodermis, lo cual afecta la plasticidad y restringe su movimiento a la estela <sup>(31)</sup>.

La transferencia y removilización del Cd desde el xilema al floema es otro de los procesos cruciales en el transporte de este ion. Otros autores identificaron altas concentraciones de fitoquelatinas, glutatión y Cd en la savia del floema de *Brassica napus* y sugirieron que el floema también es un conducto para el transporte de los complejos Cd-fitoquelatina y Cd-glutatión <sup>(32)</sup>.

### **Efectos de la toxicidad por cadmio en las plantas**

Los efectos tóxicos del Cd en las plantas han sido estudiados por numerosos autores. Los principales síntomas visibles que causa la toxicidad por Cd son la clorosis y el enrollamiento en las hojas. La clorosis puede aparecer por intercambio del Cd con el Fe o el Mg <sup>(13)</sup>,

afectándose en este último caso la estabilidad y biosíntesis de las clorofilas. Daños asociados también con la clorosis son la deficiencia de P y la reducción en el transporte de Mn<sup>(33)</sup> La reducción en el crecimiento y actividad fotosintética, el desbalance nutricional, el estrés oxidativo y las afectaciones en las actividades enzimáticas son los daños más acentuados que se expresan frecuentemente en los diferentes estudios de toxicidad con Cd (Tabla 1).

**Tabla 1.** Efectos del Cd en los procesos fisiológicos de diversos cultivos

	<b>Efectos fisiológicos</b>	<b>Plantas</b>	<b>Referencia</b>
Reducción en el crecimiento y desarrollo	Reducción de la longitud de la raíz, el área foliar y la biomasa fresca de raíz, tallo y hojas	Pimiento	(9,34)
	Reducción de la biomasa de raíz y hojas	Lechuga Rábano	(35,36)
Reducción de la actividad fotosintética	No mostró producción de frutos en 90 días.	Soya Tomate	(11)
	Reducción en el contenido de clorofilas	Guisante Papa	(37-39)
	Disminuye la Tasa Fotosintética Neta	Soya	(39)
Interfiere en la entrada y transporte de nutrientes	Reducción en el contenido de clorofilas y carotenoides	Tomate	(11)
	Reducción de la fijación de N y asimilación de NH <sub>4</sub> <sup>+</sup> en nódulos	Soya	(40)
	Reducción de las concentraciones totales de K, P, Ca, Mn, Zn, S y B	Guisante	(41)
	Reducción de Mn y aumento de Fe y Zn	Soya	(42)
	Reducción de Zn, Mn, Ca y K en el tejido foliar	Tomate	(43)
	Reducción de Mn en raíz y hojas	Tomate	(44)
	Reducción de Mn, Zn, Cu, Fe y Ca en raíz, tallo y hojas	Papa Lechuga	(45)
	Incremento de P, K, Ca Mg, Fe y Zn en tallos y hojas (Cd -1; 2,5; y 5 mg·kg <sup>-1</sup> )	Tomate Cebolla	(15)
Provoca estrés oxidativo	Reducción en condiciones de estrés más severo		
	Incremento de las concentraciones de Malondialdehído (MDA) y H <sub>2</sub> O <sub>2</sub>	Tomate	(46,47)
	Incremento de las concentraciones de MDA	Lechuga Guisante	(35-37)

En general, la presencia de Cd causa efectos variados en las actividades enzimáticas. Las enzimas que contienen grupos sulfidrilo son las más propensas a la oxidación provocada por el Cd, el mismo destruye los puentes disulfuro, provocando la desnaturalización de las

proteínas y sus consecuentes actividades enzimáticas<sup>(12,13)</sup>. El Cd también causa inhibición en las actividades de las metaloenzimas, debido a la sustitución del mismo por metales con similar carga o tamaño como es el Zn y el Mg, este último presente en la enzima RuBisCo y su intercambio con el Cd resulta en la disociación de la enzima en subunidades<sup>(13)</sup>.

Varios autores han sugerido que la toxicidad por Cd provoca estrés oxidativo en las plantas, ya sea por un incremento exagerado de la producción de especies reactivas de oxígeno, o por un déficit de la respuesta antioxidante<sup>(48)</sup>. Sin embargo, otros autores opinan que el Cd no actúa directamente en la producción de especies reactivas de oxígenos<sup>(49)</sup>.

### **Mecanismos de tolerancia al estrés por cd**

Las adaptaciones específicas de las plantas al estrés por Cd se basan en dos estrategias principales; algunas evitan o regulan la entrada y el transporte del mismo y otras toleran determinados contenidos de Cd, a través de su detoxificación, mediante quelación en orgánulos intracelulares<sup>(17,18)</sup>. Otros mecanismos de tolerancia son, el aumento del sistema de defensa antioxidante, la homeostasis celular<sup>(50)</sup>, el aumento de la producción endógena de reguladores del crecimiento vegetal y la modificación del metabolismo en función de reparar la estructura celular dañada<sup>(51,52)</sup>.

Las plantas evitan la entrada de Cd inmovilizándolo en la pared celular de las raíces a través de enlaces con exudados extracelulares, como ácidos poligalacturónidos y esto limita su transporte a la parte aérea<sup>(53)</sup>. Otras plantas han desarrollado tolerancia al estrés, acumulando los metales en las hojas, en forma de complejos metálicos estables no tóxicos, con diferentes quelantes: ácidos orgánicos, aminoácidos, ferritinas, fitoquelatinas y metalotioneínas. Estudios han mostrado que las vacuolas son el sitio de acumulación de metales pesados incluyendo el Zn y Cd<sup>(54)</sup>.

Dentro de los diferentes quelantes en plantas, las fitoquelatinas han mostrado mayor capacidad de formar complejos con el Cd, de ahí que han sido objeto de análisis en varios estudios de tolerancia. Las plantas que sobreexpresan la enzima fitoquelatina sintasa mostraron una mayor tolerancia frente al Cd<sup>(55)</sup>.

También se ha demostrado que la exposición de las plantas al Cd resulta en un incremento en la asimilación de sulfato<sup>(56)</sup> y en la actividad de enzimas involucradas en la biosíntesis del GSH, sustrato de partida en la síntesis de fitoquelatinas<sup>(57)</sup>. Se han identificado dos líneas

celulares de plantas de tomate tolerantes al Cd, y su capacidad de tolerancia depende de la potencialidad de las células de sintetizar fitoquelatinas, y formar complejos con el Cd <sup>(58)</sup>.

Sin embargo, otras evidencias indican que el incremento en la producción de fitoquelatinas no es el responsable de la tolerancia elevada al Cd en algunas plantas, ya que ambas poblaciones, sensibles y tolerantes producen cantidades equivalentes de fitoquelatinas cuando se exponen a iguales concentraciones de Cd <sup>(59)</sup>. Además de las fitoquelatinas, otros aminoácidos y vitaminas también han mostrado alteraciones frente al Cd, se observó un incremento de los contenidos de a-tocoferol, asparagina, tirosina y prolina en diferentes cultivares de tomate expuestos a estrés por este metal <sup>(49,60)</sup>.

Un caso extremo de la estrategia de acumulación es el de las plantas hiperacumuladoras, que pueden superar en 100 o más veces los valores normales de metales encontrados en la parte aérea. Las plantas en su mayoría contienen niveles medibles de Cd principalmente en la raíces, pero cuando superan el umbral establecido de  $10 \mu\text{g}\cdot\text{g}^{-1}$  (0,01 % de masa seca) se consideran hiperacumuladoras de este metal <sup>(61)</sup>. La hiperacumulación ocurre en familias no relacionadas. La mayoría de las especies y las de mayor capacidad de absorción se han encontrado en sitios de origen natural ricos en metales, entre las mismas se identifican *Arabidosisalleri*, *Thlaspirotundifolium* y *praecox*, *Sedumalfredii*, *Salsolakali* y *Viola baoshanensis*, pero también un gran número de ellas crecen en suelos limpios como son *Solanumnigrum* y *Rorippa globosa* <sup>(62)</sup>.

Se ha demostrado que en el cultivo del tomate la acumulación y tolerancia al estrés por Cd depende de la variedad. Las variedades más tolerantes, Río Grande y otra no referida, se evaluaron, respectivamente, en otras investigaciones para su posible utilización en la fitoremediación de suelos contaminados <sup>(63,64)</sup>. En ambos estudios el tomate se comportó como una planta excluyente, con una mayor concentración de Cd en las raíces ( $13,4 \mu\text{g}\cdot\text{g}^{-1}$  y  $4,3 \text{mg}\cdot\text{kg}^{-1}$ ). Según investigaciones, la variedad en estudio, solo puede acumular Cd en suelos con bajos niveles del metal porque su capacidad de acumulación disminuye con el aumento de la contaminación. También el cultivar Shenbaofen-2 es tolerante y se identificó como hiperacumulador de Cd, acumuló cantidades de 144 y  $130 \text{mg}\cdot\text{kg}^{-1}$  en raíces y tejidos aéreos respectivamente <sup>(26)</sup>.

Sin embargo, la variedad de tomate Tres Cantos, originaria de Tenerife, no se identificó como hiperacumuladora o con potencial en la fitoextracción, pero los resultados indicaron que

desarrolló mecanismos de tolerancia en los procesos de absorción y distribución de nutrientes, y conservó su crecimiento sin afectar la producción de biomasa <sup>(65)</sup>.

Otras variedades mostraron menor tolerancia que las anteriores, ya que no mantuvieron su producción de biomasa sin afectación, pero a pesar de ello no se identificaron como variedades sensibles. Dentro de este grupo se encuentran las variedades 4641 y Yufen 109 que acumularon respectivamente 2,316 y 2,237 mg·kg<sup>-1</sup> de Cd en frutos <sup>(66)</sup>. Otro estudio en estos cultivares confirmó sus capacidades de traslocación, ya que el Cd se acumuló principalmente en hojas y tallos, y la variedad 4641 mostró mayor resistencia al estrés que la Yufen 109 <sup>(67)</sup>. La variedad Ibiza F1 también se incluye dentro de este grupo, con la diferencia que desarrolló la exclusión como mecanismo de tolerancia. La mayor concentración de Cd se encontró en las raíces, pero su acumulación en este órgano y en hojas aumentó con el aumento de los niveles de Cd en solución <sup>(68)</sup>.

Por otra parte, la variedad de tomate Rutgers se identificó como una especie no tolerante de Cd y Zn <sup>(69)</sup>. También, el cultivar Navodaya se identificó como sensible a altas dosis de Cd y la fase de floración mostró mayor sensibilidad que la de fructificación <sup>(70)</sup>.

Otros autores evaluaron el grado de tolerancia al Cd de 10 variedades de tomate y en todos los casos observaron reducciones en los indicadores de crecimiento y desarrollo, pero cada cultivar mostró una capacidad inherente para tolerar el estrés por Cd. Las variedades K-25, K-21 y NTS-9 mostraron la máxima resistencia, las variedades Kaveri, NbR-Uday y Swarnodya fueron moderadamente afectadas, las variedades Sarvodya, NBR-Uttam y Malti experimentaron daños severos y la variedad S-22 no sobrevivió en presencia de Cd <sup>(71)</sup>.

Un estudio similar al anterior se realizó en 100 genotipos de tomate. Los genotipos 9086, Roma, Sitara TS-01, pak0010990, CLN-2123A, PICDENEATO, 0.006231 y 7035 mostraron los mejores rendimientos mientras que los genotipos 42-07, 17883, BL-1176-Riostone-1-1, MARMANDE y 17882 mostraron rendimientos bajos. En ambos grupos la mayor concentración de Cd fue en los tejidos aéreos respecto a la raíz, los genotipos tolerantes lo acumularon principalmente en los brotes y los sensibles en el fruto. Ambos resultados confirman que la tolerancia al estrés por Cd tiene respuesta varietal en cultivos como el del tomate <sup>(72)</sup>.



## **Estrategias para mitigar el estrés por cadmio**

Debido a los daños que ocasionan la toxicidad por Cd en las plantas y el riesgo que provoca su acumulación en ellas, varios grupos de investigación han propuesto diferentes estrategias para aminorar sus efectos. La mayoría de las estrategias incluyen realizar modificaciones en el manejo de la nutrición. Pero otras prácticas también han mostrado resultados favorecedores, tales como, la inoculación con bacterias beneficiosas <sup>(20)</sup>, los injertos sobre patrones resistentes <sup>(21,22)</sup>, la adición de diferentes reguladores del crecimiento <sup>(23,24)</sup> y la aplicación de enmienda en el suelo.

Son muchos los autores que sugieren la optimización en el manejo de nutrientes como una estrategia útil para atenuar la toxicidad por Cd, una revisión en el tema fue realizada por un colectivo de autores en el 2012 <sup>(19)</sup>.

Investigaciones posteriores en otros cultivos y otros elementos, continuaron promoviendo la adecuada nutrición como vía para mitigar el estrés por Cd. Entre los diferentes nutrientes el P, K, S, Fe y Zn mostraron significativos efectos favorables. La aplicación de P en plantas de trigo incrementó la biomasa de los brotes, el área de las hojas, el contenido de pigmentos fotosintéticos y, a su vez, favoreció la asimilación de otros nutrientes, tales como K, Ca, Mg y Mn. También aumentó la actividad de enzimas antioxidantes y disminuyó el contenido de Cd y H<sub>2</sub>O<sub>2</sub> en los brotes <sup>(73)</sup>.

Por otra parte, la adición de K redujo la absorción y traslocación de Cd en plantas de girasoles e inhibió el incremento en la permeabilidad de las membranas provocado por el estrés. Sin embargo, en este estudio no se observaron efectos en la biomasa por órganos, ni en el contenido de pigmentos fotosintéticos <sup>(74)</sup>, aun cuando en otra investigación se planteó que el K participa en la formación de pigmentos fotosintéticos y previene la descomposición de clorofilas <sup>(75)</sup>.

Del mismo modo, el suplemento de KCl en plantas de arroz cultivadas con altas concentraciones de CdCl<sub>2</sub> aumentó su crecimiento y disminuyó la actividad de la enzima NADPH oxidasa <sup>(76)</sup>. Sin embargo, otros resultados demostraron que la deficiencia de K protege a las plantas de arroz de un posterior estrés oxidativo provocado por el Cd, ya que aumenta las actividades de enzimas antioxidantes (superóxido dismutasa, ascorbato peroxidasa, glutatión reductasa y catalasa).

A diferencia de la suficiencia de K, su deficiencia no inhibe la entrada de Cd a la planta <sup>(77)</sup>. Los resultados mostraron que tanto la suficiencia como la deficiencia de K tienen efectos positivos para mitigar el estrés por Cd, pero con diferentes consecuencias cada uno. De manera similar al K, la deficiencia de Mg, Ca y N permite la activación previa de la defensa antioxidante, pero no evita la absorción de Cd por las raíces <sup>(78-80)</sup>.

En el caso del S, algunos autores plantean que está involucrado en la biosíntesis de agentes detoxificantes de metales pesados <sup>(81)</sup>. En mostaza (*Brassicajuncea*) la aplicación de 30  $\mu\text{M}$  y 300  $\mu\text{M}$  de S aminoró la afectación en el contenido de clorofila y aumentó las actividades de las enzimas antioxidantes, ascorbatoperoxidasa, glutatión reductasa y catalasa <sup>(82)</sup>.

Numerosos estudios han mostrado que una adecuada nutrición de Fe puede mitigar la toxicidad por Cd. La aplicación exógena de Fe disminuyó la concentración de Cd en plantas de tomate y arroz <sup>(67,76)</sup> y existen criterios de que una concentración adecuada de Fe puede promover la fotosíntesis y la transpiración, así como aumentar la masa seca de cada órgano en plantas de tomate <sup>(67)</sup>. Por otra parte, la aplicación foliar del complejo Zn-lys en trigo, aumentó la fotosíntesis, el rendimiento del grano, las actividades enzimáticas y redujo el estrés oxidativo y el contenido de Cd en los diferentes órganos de la planta <sup>(83)</sup>.

Además de los macro y micronutrientes analizados, existen otros elementos como el La, Se y Si, que han mostrado efectos favorables en la mitigación del estrés por Cd. Un estudio en dos variedades de tomate (var 4641 y Yufen109) enriquecidas con Cd, mostró que la aplicación de 10 y 20  $\text{mg}\cdot\text{L}^{-1}$  de  $\text{LaCl}_3$  reduce la concentración de Cd en hojas, tallo, raíces y frutos, y como consecuencia también disminuye los daños ocasionados por el Cd en el crecimiento y rendimiento <sup>(14)</sup>.

Otro estudio, que se basa en el pre-tratamiento con diferentes formas de selenio (selenocisteína, selenito y selenato de sodio), indujo la biosíntesis de la melatonina. A su vez, la presencia de Se y la melatonina aumentaron la tolerancia al Cd, con reducciones en la disminución del crecimiento, la foto-inhibición y la pérdida de electrolitos <sup>(84)</sup>.

El Si no se considera un nutriente esencial, pero sí un elemento beneficioso para mantener el crecimiento en ambientes de estrés. Frente a la toxicidad por Cd también ha aumentado la resistencia de diversos cultivos. En plantas de maní, tomate y pepino disminuyó la concentración de Cd en los brotes y hojas, pero los mecanismos implicados en ello fueron diferentes para cada especie. En tomate y maní se redujo el transporte de Cd de la raíz a las hojas y en pepino disminuyó la absorción de Cd por las raíces <sup>(85,86)</sup>.

Sin embargo, otros autores demostraron que en tomate la presencia de Si en el suelo (25, 50 y 75 mg·kg<sup>-1</sup>) provocó la precipitación de Cd en el mismo y consecuentemente la reducción de su biodisponibilidad para la captación por las raíces<sup>(87)</sup>. Aplicaciones de CaSiO<sub>3</sub> en plantas ornamentales de amaranto (*Amaranthushypochondriacus*L) redujo la concentración de Cd en la raíz, tallo y hojas e incrementó la masa seca y el contenido de pigmentos fotosintéticos. El aumento del contenido de Cd en los cloroplastos y el cambio de iones libres a formas inactivas secuestradas en compartimentos celulares fueron otras ventajas asociadas también con el CaSiO<sub>3</sub><sup>(88)</sup>.

Otro estudio evidenció que la aplicación de Si en *Arabidopsisthaliana* redujo un 50 % el contenido de Cd absorbido por la planta y aumentó la actividad enzimática antioxidante. El análisis proteómico de este estudio permitió concluir que el Si tiene una participación activa en los mecanismos implicados en la tolerancia frente al Cd<sup>(89)</sup>. Por otra parte, el pre-tratamiento de plantas de trigo con ácido salicílico 50 μM contribuyó a mantener el crecimiento de las plantas a niveles cercanos al control. También este pre-tratamiento reguló la concentración de ácido absísico y ácido idolacético que son sustancias afectadas por el Cd<sup>(90)</sup>.

## CONCLUSIONES

- La toxicidad por Cd reduce el crecimiento, la actividad fotosintética, el contenido de clorofilas y provoca clorosis principalmente en hojas jóvenes. También, interfiere en la entrada y transporte de nutrientes y ocasiona estrés oxidativo y afectaciones en las actividades enzimáticas.
- La formación de complejos entre el Cd y proteínas generalmente azufradas son el principal mecanismo de tolerancia de las plantas ante la toxicidad por este metal. A través de la formación de estos complejos las plantas evitan o regulan la entrada y transporte del Cd o detoxifican el metal y toleran determinados contenidos en orgánulos intracelulares.
- La respuesta a la toxicidad por Cd en plantas de tomate depende de la variedad, algunas variedades no sobreviven en presencia de Cd y otras, sin embargo, son tolerantes e incluso clasifican como hiper acumuladoras del metal.

- El manejo de nutrientes es una de las estrategias más eficientes para aminorar los efectos del Cd en las plantas. Los estudios realizados en este tema solo evalúan los efectos de determinados nutrientes independientes y no se evalúan los efectos simultáneos de la combinación de varios de ellos.

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Bibliographic review

## **Toxicity of Cadmium in plants and strategies to reduce its effects. Case study: The tomato**

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### **ABSTRACT**

Cadmium (Cd) is one of the most toxic heavy metals. Its high mobility and bioaccumulative power differentiate it from the rest of its group and motivate the interest of scientists to know its effects and interaction with plants. In the present work, a bibliographic review of the main mechanisms of entry and transport of the Cd in the plants and their toxic effects in them was carried out. Also, issues such as the defense mechanisms of plants against Cd stress and existing strategies to reduce their toxicity are addressed. Within the different crops, tomato is of special interest, because it is the most widespread vegetable in the world and has been shown to be a plant tolerant to Cd and with potential for its accumulation.

**Key words:** heavy metals, relationship, vegetables

## INTRODUCTION

Cadmium is a highly toxic transition metal at very low exposure levels and has acute and chronic effects on the health of plants, animals, humans and all living things in general. Because of industrial activity and anthropization, it is estimated that 30.000 tons of Cd are released into the environment every year <sup>(1)</sup>. Therefore, in different parts of the planet and in our country, Cd levels have been in water, soil and plants, detected that exceed the permissible limits established for different uses <sup>(2-7)</sup>.

Cadmium is not degradable in nature, so once released to the environment it will remain in circulation. This property together with its high mobility, bioaccumulative power and toxicity at very low concentrations make it one of the most important heavy metals. In the 1960s, environmental contamination with this metal became apparent when in Japan more than 100 people died from a disease named Itai-Itai, which was caused by high concentrations of Cd in the Jinzu River, in rice ( $4.2 \text{ mg L}^{-1}$ ) and consequently in the human body <sup>(8)</sup>. These facts motivated the interest of soil and plant science to know and control the effects that metal produced in different crops.

This metal is as one of the most toxic and inhibitory of the physiological processes of plants recognized. Studies in several crops have shown that it reduces growth, photosynthetic activity, perspiration and chlorophyll content <sup>(9-12)</sup>. In addition, it causes chlorosis, oxidative stress, and nutritional imbalances and modifies the activity of enzymes, involved in the metabolism of organic acids and in the Krebs cycle <sup>(13-16)</sup>. In general, the effects caused in some physiological processes can be so marked that plants are not able to evade them and manifest themselves in other processes. The toxicity of Cd can lead to the death of the plant and this depends, among other factors, on the exposure time, the metal content and the specific adaptations they develop.

The specific adaptations of plants to Cd stress are two main mechanisms based on. Some prevent or regulate the entry and transport of the same <sup>(17)</sup> and others tolerate certain contents of Cd, through its detoxification, by chelation in intracellular organelles <sup>(18)</sup>. Based on these tolerance mechanisms, several research groups have proposed different strategies to lessen the effects of Cd on plants. Most strategies include making changes in nutrition management

(19). Nevertheless, other practices have also shown favorable results, such as inoculation with beneficial bacteria (20), grafts on resistant patterns (21, 22), addition of different growth regulators (23, 24) and application of amendment in the soil.

Knowing the interaction of Cd with plants, as well as the search for alternatives to minimize its effects have caught the interest of the scientific community, product of the accelerated growth of contamination with this metal and its high toxicity. The objective of this study is to make an updated review of research results related to these aspects.

Within the different crops, tomato is of special interest, because it is the most widespread vegetable in the world and of greater economic value. It has been not only as food used, but also as a model plant in dissimilar research. The tomato plant has many interesting features, such as fleshy fruit, a sympodial bud and compound leaves, which other model plants (for example, rice and Arabidopsis) do not have (25). In addition, some of its varieties have shown to be a Cd tolerant plant, with potential for accumulation (26).

### **Cadmium absorption and transportation in plants**

Cd enters the plant mainly in the form of  $Cd^{2+}$ , since its chelated ions are generally not available for root absorption. The epidermal cell layer is the first tissue for ion uptake and within it; radical hairs are the most active area to absorb ions from the soil and is the structure that facilitates the absorption of  $Cd^{2+}$  (27).

Three different routes of Cd entry into the root have been proposed (28):

*First way:* in the plasma membrane of the epidermal cells of the root,  $CO_2$  (ac) dissociates into  $H^+$  and  $HCO_3^-$ , through plant respiration. The  $H^+$  is with the  $Cd^{2+}$  exchanged, of the soil and the metal adsorbs on the surface of the epidermal cells of the root. This adsorption process is rapid and does not require energy and is the stage preceding the subsequent absorption of  $Cd^{2+}$  in the epidermis through the apoplast pathway.

*Second way:* the Cd is a non-essential element and, therefore, it is assumed that the plants do not have specific input mechanisms for it. It enters the plant cells through the  $Fe^{2+}$ ,  $Zn^{2+}$  and  $Ca^{2+}$  essential metal transporters, as is the case with IRT1 and LCT<sub>1</sub> proteins. After combined with the transporter proteins, the Cd enters the epidermis layer of the root, through the path of the simplast.

*Third way:* to increase the availability of ions in the rhizosphere soil, the roots of plants secrete compounds of low molecular mass, such as mugineic acids (MA), which form complexes with  $\text{Cd}^{2+}$ . Therefore,  $\text{Cd}^{2+}$  enters the root epidermis layer through YSL-like proteins in the form of chelates.

The movement of Cd from the root to the stem is through three processes controlled: the sequestration of metals within the root cells; the transport to the wake and the release of the metal to the xylem <sup>(29)</sup>. Retention is the product of apoplastic barriers and chelation in vacuoles; it demonstrated that phytochelatins and other thiols are the main chelators in the kidnapping of Cd at the root <sup>(30)</sup>. Another of the proposed mechanisms of Cd retention in roots is through the impregnation of the suberine in the cell wall during the maturation of exodermis and endodermis, which affects the plasticity and restricts its movement to the wake <sup>(31)</sup>.

The transfer and remobilization of the Cd from the xylem to the phloem is another crucial process in the transport of this ion. Other authors identified high concentrations of phytochelatins, glutathione and Cd in the sap of the *Brassic napus* phloem and suggested that the phloem is also a conduit for the transport of the Cd-phytochelatin and Cd-glutathione complexes <sup>(32)</sup>.

### **Effects of toxicity per cadmium on plants**

Numerous authors have studied the toxic effects of Cd on plants. The main visible symptoms caused by Cd toxicity are chlorosis and leaf curl. Chlorosis may appear by exchanging Cd with Fe or Mg <sup>(13)</sup>, in the latter case affecting the stability and biosynthesis of chlorophylls. Damages also associated with chlorosis are P deficiency and reduction in the transport of Mn <sup>(33)</sup>.

The reduction in photosynthetic growth and activity, nutritional imbalance, oxidative stress and effects on enzymatic activities are the most pronounced damages that are in the different studies of toxicity with Cd frequently expressed (Table 1).



**Table 1.** Effects of Cd on the physiological processes of various crops

	<b>Physiological effects</b>	<b>Plants</b>	<b>Reference</b>
<b>Reduction in growth and development</b>	Reduction of root length, leaf area and fresh root, stem and leaf biomass	Pepper	(9,34)
	Root and leaf biomass reduction	Lettuce Radish	(35,36)
<b>Photosynthetic activity reduction</b>	It showed no fruit production in 90 days.	Soy	(11)
	Reduction in chlorophyll content	Tomato	(11)
	Decrease Net Photosynthetic Rate	Pea Potato Soy	(37-39)
<b>Interferes in the entry and transport of nutrients</b>	Decrease Net Photosynthetic Rate	Soy	(39)
	Reduction in the content of chlorophylls and carotenoids	Tomato	(11)
	Reduction of N fixation and assimilation of NH <sub>4</sub> <sup>+</sup> in nodules	Soy	(40)
	Reduction of total concentrations of K, P, Ca, Mn, Zn, S and B	Pea	(41)
	Reduction of Mn and increase of Fe and Zn	Soy	(42)
	Reduction of Zn, Mn, Ca and K in the leaf tissue	Tomato	(43)
	Mn reduction in root and leaves	Tomato	(44)
<b>Provokes oxidative stress</b>	Reduction of Mn, Zn, Cu, Fe and Ca in root, stem and leaves	Potato Lettuce	(45)
	Increase in P, K, Ca Mg, Fe and Zn in stems and leaves (Cd-1; 2.5; and 5 mg kg <sup>-1</sup> )	Tomato	(15)
	Reduction in more severe stress conditions	Onion	(15)
	Increased concentrations of Malondialdehyde (MDA) and H <sub>2</sub> O <sub>2</sub>	Tomato	(46,47)
	Increase in MDA concentrations	Lettuce Pea	(35,37)

In general, the presence of Cd causes varied effects on enzyme activities. Enzymes containing sulfhydryl groups are the most prone to oxidation caused by Cd, it destroys the disulfide bridges, causing protein denaturation and its consequent enzymatic activities <sup>(12,13)</sup>. The Cd also causes inhibition in the activities of the metalloenzymes, due to the substitution of it with metals with similar load or size such as Zn and Mg, the latter present in the enzyme Rubisco and its exchange with the Cd results in dissociation of the enzyme in subunits <sup>(13)</sup>. Several authors have suggested that Cd toxicity causes oxidative stress in plants, either by an exaggerated increase in the production of reactive oxygen species, or by a deficit in the antioxidant response <sup>(48)</sup>. However, other authors believe that Cd does not act directly in the production of reactive oxygen species <sup>(49)</sup>.

## Stress tolerance mechanisms for cd

The specific adaptations of plants to Cd stress are two main strategies based on; some prevent or regulate the entry and transport of the same and others tolerate certain contents of Cd, through its detoxification, by chelation in intracellular organelles <sup>(17, 18)</sup>. Other tolerance mechanisms are, the increase of the antioxidant defense system, cell homeostasis <sup>(50)</sup>, the increase in endogenous production of plant growth regulators and the modification of metabolism in function of repairing the damaged cell structure <sup>(51,52)</sup>.

The plants prevent the entry of Cd by immobilizing it in the cell wall of the roots through links with extracellular exudates, such as polygalacturonide acids and this limits their transport to the aerial part <sup>(53)</sup>. Other plants have developed tolerance to stress, accumulating metals in the leaves, in the form of stable non-toxic metal complexes, with different chelants: organic acids, amino acids, ferritins, phytochelatins and metallothioneins. Studies have shown that vacuoles are the site of heavy metal accumulation including Zn and Cd <sup>(54)</sup>.

Within the different chelants in plants, phytochelatins have shown greater capacity to form complexes with the Cd, hence they have been subject to analysis in several tolerance studies. Plants that overexpress the enzyme phytochelatin synthase showed a greater tolerance against Cd <sup>(55)</sup>.

It has also been shown that plant exposure to Cd results in an increase in sulfate assimilation <sup>(56)</sup> and in the activity of enzymes involved in the biosynthesis of GSH, the starting substrate in the synthesis of phytochelatins <sup>(57)</sup>. Two cell lines of tomato plants tolerant to Cd have been identified and their tolerance capacity depends on the potential of cells to synthesize phytochelatins, and complex with Cd <sup>(58)</sup>.

However, other evidence indicates that the increase in the production of phytochelatins is not responsible for the high tolerance to Cd in some plants, since both sensitive and tolerant populations produce equivalent amounts of phytochelatins when exposed to equal concentrations of Cd <sup>(59)</sup>. In addition to phytochelatins, other amino acids and vitamins have also shown alterations against Cd, an increase in the contents of  $\alpha$ -tocopherol, asparagine, tyrosine and proline was observed in different tomato cultivars exposed to stress by this metal <sup>(49, 60)</sup>.

An extreme case of the accumulation strategy is that of hyperaccumulating plants, which can exceed 100 or more times the normal values of metals found in the aerial part. Plants mostly contain measurable levels of Cd mainly in the roots, but when they exceed the established

threshold of  $10 \mu\text{g g}^{-1}$  (0.01 % dry mass) they are considered hyperaccumulators of this metal <sup>(61)</sup>. Hyperaccumulation occurs in unrelated families. Most species and those with greater absorption capacity have been found in naturally occurring sites rich in metals, among them *Arabidosishalleri*, *Thlaspirotundifolium* and *praecox*, *Sedumalfredii*, *Salsolakali* and *Viola baoshanensis* are identified, but also a large number of them grow in clean soils such as *Solanumnigrum* and *Rorippa globosa* <sup>(62)</sup>.

It has been shown that in tomato cultivation the accumulation and tolerance of stress due to Cd depends on the variety. The most tolerant varieties, Río Grande and other non-referred were evaluated, respectively, in other investigations for their possible use in the phytoremediation of contaminated soils <sup>(63, 64)</sup>. In both studies, the tomato behaved like an exclusive plant, with a higher concentration of Cd in the roots ( $13.4 \mu\text{g g}^{-1}$  and  $4.3 \text{ mg kg}^{-1}$ ). According to research, the variety under study can only accumulate Cd in soils with low metal levels because its accumulation capacity decreases with increasing pollution. In addition, cultivating Shenbaofen-2 is tolerant and identified as a Cd hyperaccumulator, accumulated amounts of 144 and  $130 \text{ mg kg}^{-1}$  in roots and aerial tissues respectively <sup>(26)</sup>.

However, Tres Cantos tomato variety, originally from Tenerife, was not identified as a hyperaccumulator or with potential for phytoextraction, but the results indicated that it developed tolerance mechanisms in the processes of nutrient absorption and distribution, and preserved its growth without affect biomass production <sup>(65)</sup>.

Other varieties showed lower tolerance than the previous ones, since they did not maintain their biomass production without affectation, but they were not as sensitive varieties identified. Within this group are varieties 4641 and Yufen 109 that accumulated respectively 2,316 and  $2,237 \text{ mg kg}^{-1}$  of Cd in fruits <sup>(66)</sup>. Another study in these cultivars confirmed their translocation capabilities, since Cd accumulated mainly in leaves and stems, and the 4641 variety showed greater resistance to stress than Yufen 109 <sup>(67)</sup>. The Ibiza F1 variety is also included within this group, with the difference that developed the exclusion as a tolerance mechanism. The highest concentration of Cd was found in the roots, but its accumulation in this organ and in leaves increased with increasing levels of Cd in solution <sup>(68)</sup>.

On the other hand, the Rutgers tomato variety was as a non-tolerant species of Cd and Zn identified <sup>(69)</sup>. In addition, the Navodaya cultivar was as sensitive to high doses of Cd identified and the flowering phase showed greater sensitivity than fruiting <sup>(70)</sup>.

Other authors evaluated the degree of tolerance to Cd of 10 tomato varieties and in all cases observed reductions in growth and development indicators, but each cultivar showed an inherent ability to tolerate Cd stress. Varieties K-25, K -21 and NTS-9 showed maximum resistance, the Kaveri, NbR-Uday and Swarnodya varieties were moderately affected, the Sarvodya, NBR-Uttam and Malti varieties experienced severe damage and the S-22 variety did not survive in the presence of Cd <sup>(71)</sup>.

A study similar to the previous one was in 100 tomato genotypes conducted. Genotypes 9086, Roma, Sitara TS-01, pak0010990, CLN-2123A, PICDENEATO, 0.006231 and 7035 showed the best yields while genotypes 42-07, 17883, BL-1176-Riostone-1-1, MARMANDE and 17882 showed low yields in both groups the highest concentration of Cd was in the aerial tissues with respect to the root, the tolerant genotypes accumulated mainly in the buds and the sensitive ones in the fruit. Both results confirm that Cd stress tolerance has a varietal response in crops such as tomato <sup>(72)</sup>.

### **Strategies to mitigate stress by cadmium**

Due to the damage caused by Cd toxicity in plants and the risk caused by their accumulation in them, several research groups have proposed different strategies to reduce their effects. Most strategies include making changes in nutrition management. However, other practices have also shown favorable results, such as inoculation with beneficial bacteria <sup>(20)</sup>, grafts on resistant patterns <sup>(21, 22)</sup>, the addition of different growth regulators <sup>(23, 24)</sup> and the application of amendment in soil.

Many authors suggest the optimization of nutrient management as a useful strategy to mitigate Cd toxicity. A group of authors carried out a review on the subject in 2012 <sup>(19)</sup>. Subsequent research in other crops and other elements continued to promote adequate nutrition as a way to mitigate Cd stress. Among the different nutrients P, K, S, Fe and Zn showed significant favorable effects. The application of P in wheat plants increased the biomass of the shoots, the leaf area, and the content of photosynthetic pigments and, in turn, favored the assimilation of other nutrients, such as K, Ca, Mg and Mn. It also increased the activity of antioxidant enzymes and decreased the content of Cd and H<sub>2</sub>O<sub>2</sub> in the outbreaks <sup>(73)</sup>.

On the other hand, the addition of K reduced the absorption and translocation of Cd in sunflower plants and inhibited the increase in membrane permeability caused by stress.

However, in this study no effects were observed on organ biomass, nor on the content of photosynthetic pigments <sup>(74)</sup>, although in another investigation it was proposed that K participates in the formation of photosynthetic pigments and prevents the decomposition of chlorophylls <sup>(75)</sup>.

Similarly, the KCl supplement in rice plants grown with high concentrations of CdCl<sub>2</sub> increased its growth and decreased the activity of the enzyme NADPH oxidase <sup>(76)</sup>. However, other results showed that K deficiency protects rice plants from subsequent oxidative stress caused by Cd, as it increases the activities of antioxidant enzymes (superoxide dismutase, ascorbate peroxidase, glutathione reductase and catalase).

Unlike K sufficiency, its deficiency does not inhibit the entry of Cd into the plant <sup>(77)</sup>. The results showed that both K deficiency and deficiency have positive effects to mitigate Cd stress, but with different consequences each. Similar to K, the deficiency of Mg, Ca and N allows the previous activation of the antioxidant defense, but does not prevent the absorption of Cd by the roots <sup>(78-80)</sup>.

In the case of S, some authors suggest that it is involved in the biosynthesis of heavy metal detoxifying agents <sup>(81)</sup>. In mustard (*Brassicajuncea*) the application of 30 µM and 300 µM of S reduced the impact on chlorophyll content and increased the activities of antioxidant enzymes, ascorbate peroxidase, glutathione reductase and catalase <sup>(82)</sup>.

Numerous studies have shown that adequate nutrition of Fe can mitigate Cd toxicity. Exogenous application of Fe decreased the concentration of Cd in tomato and rice plants <sup>(67, 76)</sup> and there are criteria that an adequate concentration of Fe can promote photosynthesis and perspiration, as well as increasing the dry mass of each organ in tomato plants <sup>(67)</sup>. On the other hand, the foliar application of the Zn-lys complex in wheat, increased photosynthesis, grain yield, enzymatic activities and reduced oxidative stress and Cd content in the different organs of the plant <sup>(83)</sup>.

In addition to the macro and micronutrients analyzed, there are other elements such as La, Se and Si, which have shown favorable effects in the mitigation of Cd stress. A study in two tomato varieties (var 4641 and Yufen109) enriched with Cd, showed that the application of 10 and 20 mg L<sup>-1</sup> of LaCl<sub>3</sub> reduces the concentration of Cd in leaves, stem, roots and fruits. Consequently it reduces the damage caused by Cd in growth and yield <sup>(66)</sup>.

Another study, which is based on pretreatment with different forms of selenium (selenocysteine, selenite and sodium selenate), induced the biosynthesis of melatonin. In turn, the presence of Se and melatonin increased tolerance to Cd, with reductions in decreased growth, photoinhibition and loss of electrolytes <sup>(84)</sup>.

The Si is not an essential nutrient considered, but it is a beneficial element to maintain growth in stressful environments. Facing the toxicity of Cd has also increased the resistance of various crops. In peanut, tomato and cucumber plants, the concentration of Cd in the shoots and leaves decreased, but the mechanisms involved in it were different for each species. In tomato and peanut the transport of Cd from the root to the leaves was reduced and in cucumber the absorption of Cd by the roots decreased <sup>(85, 86)</sup>.

However, other authors demonstrated that in tomato the presence of Si in the soil (25, 50 and 75 mg kg<sup>-1</sup>) caused the precipitation of Cd in it and consequently the reduction of its bioavailability for root uptake <sup>(87)</sup>. Applications of CaSiO<sub>3</sub> in ornamental amaranth plants (*Amaranthus hypochondriacus* L) reduced the concentration of Cd in the root, stem, leaves, and increased the dry mass and the content of photosynthetic pigments. The increase in the content of Cd in the chloroplasts and the change of free ions to inactive forms sequestered in cell compartments were other advantages also associated with CaSiO<sub>3</sub> <sup>(88)</sup>.

Another study showed that the application of Si in *Arabidopsis thaliana* reduced the content of Cd absorbed by the plant by 50 % and increased the antioxidant enzyme activity. The proteomic analysis of this study allowed us to conclude that Si has an active participation in the mechanisms involved in tolerance to Cd <sup>(89)</sup>. On the other hand, the pretreatment of wheat plants with 50- $\mu$ M salicylic acid contributed to maintain plant growth at levels close to the control. This pretreatment also regulated the concentration of abscisic acid and indoleacetic acid which are substances affected by Cd <sup>(90)</sup>.

## CONCLUSIONS

- Cd toxicity reduces growth, photosynthetic activity, and chlorophyll content and causes chlorosis mainly in young leaves. In addition, it interferes with the entry and transport of nutrients and causes oxidative stress and effects on enzymatic activities.
- The formation of complexes between Cd and generally sulfur proteins are the main mechanism of tolerance of plants to toxicity by this metal. Through the formation of these

complexes, plants prevent or regulate the entry and transport of the Cd or detoxify the metal and tolerate certain contents in intracellular organelles.

- The response to toxicity by Cd in tomato plants depends on the variety, some varieties do not survive in the presence of Cd and others, however, are tolerant and even classify as metal hyper-accumulators.
- Nutrient management is one of the most efficient strategies to reduce the effects of Cd on plants. The studies carried out on this topic only evaluate the effects of certain independent nutrients and the simultaneous effects of the combination of several of them are not evaluated.

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