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Physiological effects of postharvest UV treatments: recent progress

Pedro Marcos Civello,[1,2*] Natalia Villarreal,[3] María Eugenia Gómez Lobato[1] and Gustavo Adolfo Martínez[2,3]
[1]INFIVE (CONICET-UNLP), Instituto de Fisiología Vegetal, La Plata, Pcia Buenos Aires, Argentina
[2]Facultad de Ciencias Exactas, Universidad Nacional de La Plata (UNLP), La Plata, Pcia Buenos Aires, Argentina
[3]IIB-INTECH (CONICET-UNSAM), Instituto de Investigaciones Biotecnológicas-Instituto Tecnológico de Chascomús, Chascomús, Pcia Buenos Aires, Argentina

Purpose of review: The goal of this review is to summarize the recent progress on the effects of UV radiation on fruits and vegetables metabolism.
Main findings: Effective UV irradiation treatments can delay ripening and senescence, decrease decay and ameliorate the effects of chilling injury. The effects of the treatment on metabolism depend highly on irradiation intensity, and not only on the UV dose applied. Irradiation causes a temporary stress that significantly modifies the metabolism of fruits and vegetables, affecting the level of enzyme activities and gene expression. A complex defense response against pathogens arises in the irradiated tissue, which includes the induction of a wide range of genes and the modification of enzyme activities, as well as *de novo* synthesis of pathogenesis related proteins (PR) and the increase of secondary metabolites. Particularly, UV treatment affects oxidative metabolism and enhances the antioxidant capacity of the product, which could contribute significantly to delaying vegetable senescence, generating defense responses, and reducing chilling injury. In some cases, the radiation stimulates the synthesis of bioactive compounds that can increase the beneficial properties of fruits, vegetables and their by-products.
Limitations/implications: As the knowledge of mode of action of UV treatments increases, more efficient postharvest irradiation treatments can be designed. The finding of adequate irradiation parameters (dose, irradiation intensity) for each product, will allow applying shorter effective treatments, which are feasible for application on a commercial scale.
Directions for future research: Better understanding of the mode of action of UV radiation on plant metabolism will help to design more effective treatments. Transcriptomic and proteomic analyses of UV irradiated fruits and vegetables may contribute to identifying key steps and pathways involved in tissue responses and ultimately help to maximize the beneficial effects of UV radiation on fresh produce.

Keywords: UV; ripening; senescence; postharvest; pathogen; plant defense

Abbreviations

APX	Ascorbate Peroxidase
CAT	Catalase
LOX	Lipoxygenase
MDA	Malondialdehyde
PAL	Phenylalanine Ammonia Lyase
PAR	Pathogenesis-Related Proteins
SOD	Superoxide Dismutase

Introduction

Treatments based on UV irradiation, mainly UV-C, have been widely used with sterilization purposes in the fields of health, microbiology and food processing due to its germicidal properties. However, it is possible to apply an appropriate low dose of a potentially harmful agent such as UV radiation to induce beneficial responses in biological systems, and particularly in plant tissues; the concept underlying this strategy is known as hormesis [1, 2]. Postharvest treatment of fruits and vegetables with relatively low doses of UV radiation, particularly UV-C, have proven to be effective in delaying ripening and senescence, diminishing decay, and even in increasing the content of beneficial compounds [3-5]. A growing number of studies on the application of UV treatment in fruits and vegetables, both as whole and fresh-cut products, have been published in recent years; however, our understanding of the fundamental effects of UV irradiation on produce metabolism is still incomplete. A better understanding of the mode of action of UV treatment on produce metabolism will be helpful in the design of more efficient postharvest irradiation treatments. This review summarizes recent progress on the effects of UV radiation on fruit and vegetable metabolism.

UV treatments

The effect of UV treatment on a specific product (fruit, vegetable, fresh-cut produce) depends on many experimental factors. Some of these include the UV radiation type (UV-C, UV-B, UV-A), dose (energy per area unit, ie, kJ/m^2) and intensity (energy per area unit per time unit, ie, kJ/m^2s), the ripening or developmental stage, the cultivar, temperature, and treatment uniformity. UV-C hormetic irradiation dose ranges typically between 0.2 and 40 kJ/m^2, depending on the commodity [3, 4]. However, not only must an appropriate dose be chosen, but particular attention should also be paid to the irradiation intensity since significantly different responses could be observed depending on the radiation fluence [6].

Fruit ripening

Treatment with UV radiation has been proven to be effective in delaying postharvest fruit ripening and senescence in many fruits. In general, UV treatment can cause a general ripening delay [4, 5], but the effects are variable depending on the particular ripening-associated process under study. Some of the main effects are described in the following sections.

***Corresponding author:** Pedro Marcos Civello; Email: pmcivello@agro.unlp.edu.ar

Ethylene production

Abiotic stresses (ie, heat, wounding and oxidative stress) increase ethylene production. UV radiation is a strong oxidant, which can enhance ethylene biosynthesis in plant tissues. In most cases, ethylene production increases shortly after the irradiation treatment, while it decreases during storage. This correlates with the delay of ripening, as has been reported in Capello tomatoes [7] and strawberries, although in the latter the ethylene influence should be minor because the fruit is non-climacteric [8]. In other cases, like Flavortop tomatoes [9*], Zhenfen tomatoes [10**] and peaches [11**], ethylene production has been shown to be higher in UV-treated fruits during storage. In the case of Flavortop tomatoes the increase in ethylene production has been shown to be associated with higher expression of *ACCS* (ACC-synthase) and *ACCO* (ACC-oxidase) [9*].

In Zhenfen tomatoes an ethylene responsive element binding protein, an ethylene receptor-like protein and a ripening-related ACC synthase were induced after UV-C treatment [10**]. However, despite the increment in ethylene production, these fruits showed a delayed ripening phenotype. Interestingly, in UV-treated peaches the increment in ethylene production occurs simultaneously with a delay in softening, which was correlated with a higher level of polyamines [11**]. The results reported in the literature are quite variable and Bu *et al.* [12] reported a reduction of ethylene production in UV-C-treated tomatoes immediately after treatment and during storage. This is likely related to the large number of factors determining the outcome of UV radiation of plants as indicated above.

Respiration rate

The effect of UV radiation on fruit respiration rate is also quite variable, probably due to different effects of doses and intensities assayed. In general, under low UV-C doses the respiration rate remains unaffected or at slightly lower levels, while higher doses causes a transient increase in respiration, followed by a reduction during storage [7, 13]. Interestingly, in peaches, the reduction in respiratory activity after UV-C treatment correlated with a lower succinic dehydrogenase and cytochrome C oxidase activity suggesting lower mitochondrial activity [14].

Firmness

Fruit firmness is affected by two main factors: turgor pressure and cell wall integrity. Loss of firmness has been largely correlated with solubilization and depolymerization of cell wall constituents and expression of enzymes and proteins associated with cell wall degradation [15]. Diverse studies have shown that UV treatments can delay firmness loss in different fruits [5, 16]. In tomato, UV-C reduces the activity of cell wall degrading enzymes such as polygalacturonase, pectin methyl esterase, cellulase, xylanase and β-galactosidase [17], and suppressed the transcriptional expression of *PME2.1*, *Cel1*, *PGcat* and *Exp1* genes [12]. In strawberries, the irradiation reduced the expression of genes associated with cell wall degradation (expansins: *FaExp2*, *FaExp4* and *FaExp5*, polygalacturonase: *FaPG1*, and endoglucanase: *FaCel1*) a few hours after irradiation, while increased it afterwards to reach similar or higher levels than the controls [18]. Liu *et al.* [10**] performed a microarray analysis by using Affymetrix Tomato Genechip and found that the expression of 8 genes related to cell wall degradation was up regulated, while that of other 17 genes, including expansins and endo-β-1,4-glucanases, was down regulated.

Color and pigments

UV treatments can modify the metabolism of chlorophylls, carotenoids and anthocyanins, the three main groups of pigments contributing to fruit and vegetable color.

Carotenoids

UV radiation can affect the content of carotenoids, with the effect being highly dependent of the radiation type, dose, and the species studied. In Moneymaker tomatoes, UV-B treatment increased the concentration of carotenoids [19]. However, under the doses usually used in postharvest UV-C treatments, a reduction in carotenoid level has been observed in peppers [13] and Capello tomato [7]. In the latter case, high UV-C doses (24.4 kJ/m²) impaired ripening and caused abnormal browning, along with an overaccumulation of carotenoids [20]. In contrast, carotenoids were not affected by UV-B in treated broccoli sprouts [21**]. Finally, in Zhenzhu tomatoes, a UV-C treatment of 4.2 kJ/m² suppressed the expression of two genes involved in lycopene synthesis (*Psy 1,* phytoene synthase; *Lcy-b,* lycopene β-cyclase) resulting in fruits with abnormal color, probably due to a higher lycopene to β-carotene ratio [22].

Anthocyanins

It has been shown that UV-radiation induces phenylalanine-ammonia lyase (PAL) activity, and increases the accumulation of anthocyanins [5]. However, a lower accumulation of anthocyanins after UV-C irradiation has been also reported in strawberries [23, 24]. Li *et al.* [24] found that activities of PAL, tyrosine-ammonia lyase and *p*-coumarate ligase were immediately up-regulated with UV-C radiation, but were then inhibited, along with dihydroflavonol 4-reductase, after few days.

In some cases UV treatments can be useful in improving fruit quality. Zhang *et al.* [25*] reported that UV-B postharvest irradiation can induce anthocyanin accumulation in Red Chinese sand pears by increasing the expression of five genes associated with anthocyanin biosynthesis (*PpPAL,* PAL*; PpCHS,* chalcone synthase; *PpCHI,* chalcone isomerase; *, PpF3H,* flavanone 3-hydroxylase; and *PpANS*, anthocyanidin synthase).

Chlorophylls

UV-C based treatments can delay chlorophylls degradation, and decrease the activity of several enzymes and the expression of genes involved in their catabolism (see Senescence section). Degradation of chlorophylls is a common feature during fruit ripening that is desirable for most fruits, but is associated with quality loss in others like lime (*Citrus latifolia*). UV-B irradiation was shown to retard degreening and chlorophyll degradation in this fruit species [26]. The treatment caused a temporary increment in chlorophyllase, Mg-dechelatase and pheophytinase activities followed by a decrease after 5 days of storage at 25°C [27].

Flavor and aroma

Total sugar content and acidity are two major factors associated with fruit flavor. The effects of UV treatments on these parameters are quite variable. In most cases, under the UV doses commonly assayed, the treatments do not modify or have a slight effect on the levels of organic acids and sugars [5]. The influence of UV treatments on sugar metabolism has been scarcely analyzed. In lemons, soluble sugars (sucrose, glucose and fructose) accumulated in the peel after UV-B exposure, but the distribution patterns were different in flavedo and albedo. This effect is related to UV-B-induced changes in the activity of sucrose-hydrolyzing and -synthesizing enzymes: invertase, sucrose synthase and sucrose phosphate synthase [28].

Regarding UV effects treatments on the synthesis of volatile organic compounds (VOCs), it was observed that UV-B (both *in vitro* and under field conditions) induces grape berries to produce volatile organic compounds (mainly monoterpenes and some aldehydes, alcohols and ketones) [29]. These results might be explained, at least partially, by the induction of terpene synthases [29

-31]. Volatile organic compounds could protect grape berries from UV-B and other abiotic and biotic stresses and, importantly, could affect the wine flavor.

Antioxidants and bioactive compounds

Plants are an important source of functional foods. Fruits and vegetables included in the human diet have a large variety of antioxidants including phenolic compounds, ascorbic acid and carotenoids. Other compounds such as glucosinolates and resveratrol have attracted interest due to their anticancer activity. Significant changes in the metabolism of these compounds have been reported in response to UV irradiation. Treatments with UV-C promote the antioxidant capacity in diverse fruits and vegetables such as pepper [32], strawberry [33], tomato [34] and blueberry [35, 36]. A similar effect was found in UV-B treated apples [37], tomato [38], and black currant [39]. Extensive research has shown that both UV -C and UV-B radiation stimulates phenylpropanoid metabolism in plants [40]. It was shown that PAL activity (the key enzyme of phenylpropanoids metabolism) and expression of related genes are enhanced by UV treatment in strawberry [24], banana [41**], peach, nectarine [42, 43] and mango [44]. Moreover, other enzymes and genes such as chalcone synthase, chalcone isomerase and *p*-coumarate ligase, involved in the first stages of phenylpropanoid metabolism, were also enhanced by UV radiation [24, 42].

A particular phenolic compound, resveratrol, has acquired increased interest in recent years. Resveratrol (trans-3,5,42-trihydroxy-stilbene) is a polyphenol synthesized from cinnamic acid derivatives. It is a phytoalexin having potent antifungal properties for the plant side [5], and several benefits for human health. Resveratrol is a strong antioxidant, being able to scavenge free radicals and to inhibit low-density lipoprotein (LDL) oxidation, and has been reported to have cardioprotective and anticancer activity. In plants, resveratrol is synthesized by the enzyme stilbene synthase, which condenses one molecule of coumaroyl-CoA and three molecules of malonyl-CoA. Its presence has been reported in diverse fruits but its content is particularly high in grapes [5, 45]. UV-C treatments increased the level of resveratrol and enhanced the activity of stilbene synthase and expression of related genes in grapes [46-50*].

Another valuable compound with antioxidant capacity in fruits and vegetables is ascorbic acid. The effect of UV radiation on ascorbic metabolism is variable. UV-B treatment can increase the concentration of ascorbic acid and carotenoids in flesh and peel of tomato [19]. However, UV-C irradiation of peppers did not modify the total ascorbic concentration, even when there was an increase in the activity of ascorbate peroxidase (APX), a ascorbic acid catabolic enzyme [32]. The increase of APX activity in response to UV-C irradiation was also found in strawberry [33], banana [41**], and peach [14], and may contribute to reducing the level of ascorbic acid after irradiation. Preharvest experiments performed on tomato plants to suppress the incidence of UV-B radiation showed that the content of individual flavonoids and expression of genes involved in biosynthesis was affected. The effect was stimulant or repressive depending on the variety of tomato used and the maturity stage analyzed [51]. UV treatments can enhance antioxidant capacity of fruits and vegetables by increasing phenolic compounds. In addition, the treatments can also stimulate the enzymatic antioxidative system inducing the activity of superoxide dismutase, catalase and APX, which may contribute to keeping the levels of reactive oxygen species under control; ie, UV-C treatment reduced the levels of H_2O_2 and O_2^- in bananas [41**] and peaches [14].

Another group of nutraceutical compounds are glucosinolates. These compounds belong to a large group of secondary metabolites containing N and S and are utilized by plants in defense against herbivores. In recent years glucosinolates have received increased interest because their hydrolysis products, the isothiocyanates, have anti-carcinogenic activity [52]. Recently, it was shown that UV-B irradiation enhances glucosinolate accumulation and expression of genes related to their biosynthesis in broccoli sprouts [21**].

Chilling injury

Refrigerated storage is the most common strategy for extending postharvest life and maintaining the quality of fruits and vegetables. However, the benefits of refrigeration are limited in cold sensitive fruits because of the possible incidence of chilling injury. In many cases, UV-C treatments can reduce the incidence of this disorder, as it has been reported in peach [11**], pepper [13, 32], mango [44] , and banana [53]. The mechanisms involved in the development of chilling injury may be variable, although in many cases the disorder has been associated with oxidative stress [54]. In banana, UV-C treatment reduced membrane damage during cold storage, which correlated with lower lipoxygenase (LOX) activity and malondialdehyde (MDA) content [53]. Moreover, it was shown that chilling injury in banana is associated with oxidative stress caused by the accumulation of H_2O_2 and superoxide anion, and that UV-C treatment increased the activities of superoxide dismutase, catalase, peroxidase, APX, and glutathione reductase, resulting in fruits with reduced cellular oxidative damage, as indicated by lower MDA levels and DNA degradation [41**].

Senescence and chlorophyll degradation

Senescence is the programmed cell death process that occurs normally at the end of life of plant tissues, but it is also triggered by harvesting and the consequent stress caused by the disruption of energy, nutrients, hormones and water [55]. The main symptom of vegetable senescence is chlorophyll degradation, which causes degreening and a consequent quality loss [56]. Several UV treatments have shown their efficacy in delaying senescence and chlorophyll degradation.

UV-C treatments

Very few studies have shown the effect of UV-C treatments in delaying senescence during postharvest of green horticultural crops. Costa *et al.* [57], have shown that UV-C can delay broccoli senescence-associated processes like an increase in respiration rate and electrolyte leakage. Moreover, in Chinese Kale, these treatments reduced respiration rate and ethylene biosynthesis [58]. Oxidative processes contribute significantly to senescence and UV-C treatments enhance the antioxidant capacity of fruits and vegetables. Therefore, the delaying effect on senescence found in UV-C treated vegetables could be partially mediated by the maintenance of antioxidant capacity. UV-C irradiation reduced the degradation of ascorbic acid and increased PAL activity and the level of phenolic compounds in minimally processed broccoli [59]. The activity of enzymes involved in ROS metabolism, such as APX, superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX), increases in response to UV-C, as it was reported in minimally processed broccoli [60]. LOX activity contributes to membrane and lipid degradation during senescence. Postharvest UV-C treatment reduced LOX activity in bananas [53], but this effect was not detected in broccoli [61**].

UV-C treatment also delayed chlorophyll degradation and the activity of enzymes involved in its catabolism [57]. Few articles reported the effect of UV-C on gene expression during postharvest, and most of them correspond to genes involved in chlorophyll degradation in broccoli. UV-C irradiation reduced the expression of important genes like, Stay-Green (*SGR*) [62], Chlorophyllase 1 (*CHL1*), Pheophytinase (*PPH*) [63*], and Pheophorbide a Oxigen-

ase (*PaO*) [64]. On the other hand, an increment in Chlorophyllase 2 (*CHL 2*) expression was observed in UV-C treated broccoli florets [63*]. Also, Gómez-Lobato, *et al.* [61**] reported a lower expression of lipoxygenase 1 gene (*BoLOX1*).

UV-B treatments

The number of reports on UV-B postharvest treatments is much lower. Aiamla-or *et al.* [65**] reported that UV-B doses in the range of 8.8 - 26.3 kJ/m² delays degreening, and reduces levels of chlorophyll catabolite derivatives, such as chlorophyllide, 13²-hydroxychlorohyll *a*, pheophorbide and pyropheophorbide *a* in broccoli stored at 15°C. This effect is probably due to the lower activity of degrading chlorophyll enzymes such as chlorophyllase, chlorophyll-peroxidase Mg-dechelatase and Mg-dechelating substance [66]. This effect is similar to that described above in the flavedo of lime fruits (*Citrus latifolia Tan.)* [26]. Regarding transcripts levels, the expression of pheophytinase *(BoPPH)* gene was reduced in broccoli heads irradiated with UV-B treatment, however, there was no reduction in the expression level of two chlorophyllase genes (*BoCLH2* and *BoCLH3)*. A high expression level of pheophorbide a oxygenase (*BoPAO)* was found in senescent broccoli florets, and the up-regulation of its expression was delayed by UV-B treatment [67**].

UV-A treatments

To date only a few studies have been conducted on plant response to UV-A radiation. In cucumber (*Cucumis sativus L.*) irradiation with UV-A reduced yellowing and softening during storage at 10°C but not at 5°C [68]. Aiamla-or *et al.*, [65**]compared the effect of UV-A radiation with UV-B radiation in broccoli and observed that UV-A radiation did not delay yellowing or reduce the *Hue* angle at the doses applied (4.5 and 9.0 kJ/m²).

Defense mechanisms

As postharvest fruit decay constitutes the main cause of economic losses, the implementation of pre-storage treatments that improve fruit resistance to diseases is highly desirable. The control of postharvest diseases by UV treatment has been shown to occur through two different mechanisms; a direct germicidal effect on pathogens and induced defense mechanisms in the plant tissue [69**]. In the last few years a growing number of studies on different products have reported the induction in response to UV irradiation of: i) pathogenesis-related proteins (PR); ii) non-enzymatic and enzymatic antioxidants, and iii) phenylpropanoid biosynthetic enzymes.

Pathogenesis-related proteins (PR) are classified into 18 families (PR-1 to PR-18) on the basis of their common biochemical and physiological properties. PR proteins exhibit a wide range of defense activities as: β-1,3-glucanase and chitinase (fungal cell wall degradation); proteinase-inhibitor; defensin; lignin-forming peroxidase; thaumatin-like protein; endoproteinase; lipid-transfer protein [70*]. In tomato fruit, UV-C enhanced the synthesis of several constitutive proteins and induced *de novo* synthesis of PR proteins (such as β-1,3-glucanases, chitinases and thionin-like proteins with potential antimicrobial activity) [71]. Some authors proposed that *de novo* synthesis of these proteins and the possible induction of protease inhibitors by UV-C, may contribute to the slower rate of total protein decline detected during storage of UV-C treated fruits. A massive analysis of UV-C effect on gene expression of tomato fruit was performed by microarrays [10**]. More than 270 genes mainly involved in signal transduction, metabolism and defense response were up-regulated in tomato fruits irradiated with UV-C in comparison to untreated controls. In grapevine, the spatial and temporal accumulation of two PR proteins (chitinase and thaumatin-like protein) during berry ripening and after UV-C exposition was studied [72]. In UV-C treated berries, both PR mRNAs were strongly induced before *véraison,* and the authors proposed that chitinase and thaumatin-like protein could be key enzymes in berry defense mechanisms.

Phenolic compounds are the most abundant class of plant secondary metabolites and share a common origin in the phenylpropanoid pathway, with PAL being the first enzyme in the pathway. These metabolites (including flavonoids, tannins, hydroxycinnamate esters and structural polymer lignin) play protective roles against pathogens through direct inhibition of growth, reinforcement of plant cell walls, potential scavenger activity of free radicals and/or inactivation of pathogen enzymes that contribute to plant tissue maceration [73, 74]. Strawberry fruit irradiated with hormetic doses of UV-C showed: i) an increase in the expression and activity of PAL and peroxidase, which could be implicated in the formation of a mechanical barrier through lignin polymers synthesis and, ii) an up-regulation of several PR proteins, suggesting that the reduction in strawberry fruits decay by UV-C treatment at harvest could be related to the increase in the transcription and activity of a set of enzymes and proteins involved in the defense against pathogens like *Botrytis cinerea* [75]. It has been reported that once unripe strawberry fruits were illuminated with UV-C, PAL activity was significantly promoted on day zero and thereafter the promotion decreased [24]. A significant increase in total phenol levels was observed in the climacteric and post-climacteric phases of UV-C treated tomato fruits when compared to those of control fruits [76]. Two independent studies showed that UV-C can effectively control the infection by *B. cinerea* and *Alternaria alternata* in tomato fruits [77*] and *B. cinerea* and *Penicillium expansum* in pear fruits [78]. Moreover, UV-C treatment enhanced the biocontrol of yeast *Cryptococcus laurentii* in tomato and yeast antagonist *Candida guilliermondii* in pear, probably by the elicitation of defense response including gene up-regulation and increased activity of several PR proteins, PAL, peroxidase and catalase and superoxide dismutase. Antioxidant enzymes activities were also enhanced by UV-C in shiitake mushrooms [79].

Additionally, UV-C treatment might reduce the susceptibility to *B. cinerea* in tomato fruits by the modification of fruit surface and changes in fungal colonization. Fewer fungal adhesion structures were observed on UV-treated fruits than in control fruits suggesting that modification of epicuticular waxes could affect the capacity of *B. cinerea* to attach the fruit surface [80].

Conclusion

Postharvest treatments based on UV irradiation have received increasing attention during recent years, and a better knowledge of the mode of action of UV irradiation on produce metabolism will help to design more efficient treatments to be applied in commercial settings. Both radiation dose and intensity should be considered in optimizing UV treatments. This has been proved for UV-C, but it could be particularly important in the case of UV-B and UV-A treatments where no or slight benefits where found. Irradiation causes a temporary stress that redirects the metabolism of fruits and vegetables, both at the level of enzyme activity and gene expression. A complex defense response against pathogens arises in the irradiated produce, which includes the induction of gene expression and accumulation of pathogenesis-related proteins (PR); non-enzymatic and enzymatic antioxidants, and phenylpropanoid biosynthetic enzymes. UV affects the oxidative metabolism and enhances the antioxidant capacity of the products, which could contribute to delaying senescence, and ameliorating the effects of chilling injury. In the case of fruit ripening, the exposure to UV radiation causes a temporary increase of respiration and ethylene production, generally followed by a decrease of both during storage that could partially explain the delaying effect on softening and color development. In addition, UV radiation can promote the

synthesis of bioactive compounds. The interpretation of the effects of UV irradiation on produce metabolism would highly benefit from analyses of the modification of transcripts and proteins caused by the treatments.

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