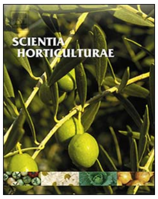
Scientia Horticulturae xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti



# UV-C light and pulsed light as alternatives to chemical and biological elicitors for stimulating plant natural defenses against fungal diseases

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## ARTICLE INFO

*Keywords:*
Elicitors
Fungal diseases
Fruits
Oxidative stress
Plant
Defenses
UV-C light
Vegetables

## ABSTRACT

UV-C light, notably under the forms of either short duration illuminations supplied by mercury vapour lamps or LEDs, or flashes of pulsed light supplied by xenon lamps, can be at the origin of inhibitory and damaging effects in plants. But when UV-C light is applied at hormetic doses, it can exert beneficial effects on plants and on harvested organs. This review, largely based on observations made on fruits and vegetables after harvest, presents direct and indirect (based on observations on the secondary metabolism) evidence that UV-C light can stimulate plant natural defenses against fungal diseases. The mechanisms of UV-C light perception and the signaling, regulatory and metabolic pathways involved are not well documented in the literature. It may however be safely hypothesized that oxidative stress plays an important role in UV-C light perception and signaling, possibly besides other mechanisms. Based of the high potential of UV-C light as an elicitor of plant defenses, especially in horticulture, the review advocates strongly in favor of increasing of our understanding of the physiological basis of UV-C effects on plants.

## 1. Introduction

Pesticides protect plants and crops against pests and diseases but the protection provided often entails health hazards for consumers and negative side effects for the environment. Moreover, pesticides must be used repeatedly to be effective, therefore favouring the emergence of resistant strains (Komarek et al., 2010). We need to develop solutions alternative or complementary to pesticides, allowing to decrease their use, therefore meeting consumer expectations for safer food and citizens expectations for reduced impact on the environment. Such solutions must be credible, i.e. efficient in a context of increasing pressure of plant pests and diseases. Chemical and biological resistance inducers (elicitors) are on the rise but their development is limited by inconsistent efficacy, as a consequence, among others, of problems of formulation and stability in field conditions.

Physical elicitors do not present these drawbacks and have the additional advantage that they can be easily combined with other existing methods of treatment, either chemical or biological. Among physical elicitors, all do not have the same potential for agriculture. Stress and notably water deficit have been advocated for being capable to stimulate plants' natural defenses. But stress and water deficit also result in a decrease in photosynthesis and yield. Other environmental factors could also be envisaged. Light for instance is an important regulator of the plant-pathogen interactions. High levels of light and UV radiations can stimulate plant defenses (Demkura and Ballaré, 2012) and the idea of using light as a physical elicitor is therefore gaining weight. The rationale behind the stimulating effect of light on plant defenses could be rather simple. In response to a sudden exposure to high light intensity or to UV radiations, plants respond by producing reactive oxygen species (ROS) that exert well-documented roles in plant defenses against pests and diseases. The rapid accumulation of hydrogen peroxide at the attack site of pathogens is directly toxic to the latter (Lamb and Dixon, 1997) and ROS can moreover trigger or be involved in signaling pathways that are responsible for the activation of other defense mechanisms, such as the production of secondary metabolites, many of which are defense compounds (Dat et al., 2000; Grant and Loake, 2000).

More specifically, UV-B radiations (280–320 nm) have been reported to increase plant resistance to leaf pathogens (Ballare et al., 2011; Demkura and Ballaré, 2012; Kuhlmann and Müller, 2010). UV-B radiation has been found to act through signaling pathways which closely resemble those for pathogen resistance (Brosché and Strid, 2003; Frohnmeyer et al., 1999; Nawrath et al., 2002). However, extensive periods of exposure, typically of several hours, even of days and

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https://doi.org/10.1016/j.scienta.2018.02.057
Received 13 October 2017; Received in revised form 12 December 2017; Accepted 21 February 2018

Please cite this article as: L, U., Scientia Horticulturae (2018), https://doi.org/10.1016/j.scienta.2018.02.057

weeks, are required for UV-B radiations to be effective. We therefore advocate for using instead UV-C radiations (200–280 nm), which are capable to supply large amounts of energy in a very short period of time (Urban et al., 2016).

We propose here to specifically focus on UV-C light, with special emphasis on UV-C light under the form of short duration illuminations, and on Pulsed Light (PL) which has an important UV-C component, generally believed to carry most of its disinfecting and arguably biological effects. Both types of illuminations allow for short, well-controlled plant treatments, well adapted to post-harvest treatments, but they could alos be used in the field with the advantage that illuminations are more or less insensitive to the climatic conditions.

## 2. UV-C light and pulsed light

Among all ultraviolet radiations of solar origin, only UV-A (320–400 nm) and UV-B (280–320 nm) radiations reaching the earth surface are expected to increase in the future since UV-C radiations are absorbed by the ozone layer (Bintsis et al., 2000). UV light can be generated through different physical processes:

1) by electrical or optical excitation of a semiconductor material,
2) by electrical or optical excitation of xenon gas or vapours of mercury,
3) more rarely by heating of a material until incandescence.

Different types of lamps are used to generate UV-C light, including light emitting diodes (LEDs), low pressure mercury vapor lamps and xenon lamps. The technologies used strongly influence the emission spectrum and the density of optical power ($W\,m^{-2}$). The latter is also strongly influenced by the distance between the lamps and the surface of plants or plant organs to be treated. Doses ($J\,m^{-2}$) are obtained as the density of optical power multiplied by the time of exposure.

### 2.1. LEDs

When exciting a semiconductor material, the wavelength emitted depends on the electronic band gap of the junction material. This essential element of the LED must be directly supplied in electricity and polarized in order to allow the circulation of a strong electronic current which is converted into optical power. The emission spectrum is narrow for LEDs as shown in Fig. 1. UV-C LEDs currently available on the market have peaks in the 262–265 nm range. They differ a lot in terms of optical efficiency. Thanks to performing optical confinement, some LEDs can now deliver 50–100 mW at 300 mA in the pulsed mode (Chrystal, 2014). With a suitable optical device, the beam can be concentrated to provide densities of optical power of 50–100 $mW\,cm^{-2}$. It must be underlined that UV-C LEDs are well-suited for generating flashes. LEDs can indeed be easily controlled through the electrical current which is supplied to them. Variable energy pulses can be generated by adapting the current supplied to LEDs and the duration of the current pulses by means of a programmable electronic impulse generator (Rothwell Jr et al., 1991).

Whereas UV-C LEDs trigger a lot of interest among LEDs-makers and potential users, references are still scarce. Also it must be underlined that they are still expensive, all the more that their life time is currently of less than 2000 h. This said, LEDs offer unique advantages. They have a great flexibility. They can notably be used to provide either continuous illuminations or flashes. Since the same electronic source can drive several LEDs simultaneously, they can be easily combined to provide customer-tailored cocktails of wavelengths (Chabane Sari et al., 2017). Eventually LEDs-based systems can be very compact and robust. For all these reasons it is our belief that they will prove irresistible as their price falls down over time.

### 2.2. Low pressure mercury vapour lamps

When gases are used for generating UV-C light, the spectrum obtained depends firstly on the nature of the gaz and secondly on its pressure. As gas pressure increases, several broad spectral lines appear. For very high pressures they merge forming a continuous spectrum. On the contrary, when gas pressure is low, the spectrum generated is a narrow-band one.

This is the case notably for low pressure mercury vapour lamps which generate a peak at 254 ± 2.5 nm. Such lamps are commonly used for disinfection purposes. They are easy to find on the market and cheap, but ignition and extinction times are of 0.5–1 s, making them more suitable for continuous exposures than for true flashes, i.e. illuminations of less than 1 s. The lamps are also shock-sensitive and they must be handled with care in rough environments.

### 2.3. Pulsed light

Pulsed light (PL) consists of a succession of very short flashes of the order of one hundred μs which are generated by an electronic oscillator discharging into xenon or xenon-mercury lamps. Xenon is a gas from column 18 of the table of chemical elements. It emits spontaneously high intensity white light, in a 185–2000 nm range, when it is excited by a strong electric discharge of the order of one kV. Xenon, when associated with mercury (xenon-mercury), provides a broad spectrum with several intense UV rays, as illustrated in Fig. 2 (Travis et al., 2010). Approximately 15–50% of the emitted energy is in the UV range (Gomez-Lopez and Bolton, 2016) but the proportion of UV-C radiations remains low ($< 1\%$). Filters can be used to retain only the UV-C part. The optical power spectral densities reachable are of the order of 10 $mW\,cm^{-2}\,nm^{-1}$ for the most powerful commercial lamps. It should be theoretically possible to achieve densities of optical power of 50 to 500 $mW\,cm^{-2}$ around 254 nm with a filter having a spectral banwidth of 50 nm and a transmittance equal to 100%. So far PL has been successfully applied for disinfection purposes in the medical field and in the food industry. The PL technology is well mastered and relatively affordable when compared to the current LED technology. A comparison between LEDs, low pressure of mercury vapour lamps and pulsed light is provided in Table 1.

## 3. Scientific background about the biological effects of UV-C light

### 3.1. Damaging effects

UV-C radiations are known since several decades for carrying inhibitory, damaging and even lethal effects and they are therefore widely used for disinfection purposes (Paul and Gwynn-Jones, 2003). There is a large amount of evidence demonstrating that UV-C light can exert antimicrobial effects, notably on bacteria (Bintsis et al., 2000; Farkas, 1998; Jay et al., 2005; Rosenstein and Ducore, 1983; Tyrrell, 1973), UV-C radiations may also exert damaging effects on higher plants (Wituszyneska et al., 2015). Direct destruction of plastoquinones (PQ) by UV-C radiations has been reported in chloroplasts (Bishop, 1961; Shavit and Avron, 1963). The action spectrum of photosystem II (PSII) damage peaks at 250–260 nm, precisely where oxidized PQ absorbs (Vass et al., 2005). There is a close similarity between the action spectrum by the absorbance of the oxidized tyrosine radicals and, to a lesser extent, by oxidized PQ, which suggests that these species are involved in sensitizing UV-C damage. Interestingly, PQ, besides carotenoids, flavonoids, tocochromanols, ascorbate and glutathione act as antioxidants, notably against singlet oxygen (Ksas et al., 2015). Damaging effects of UV light on the structure of thylakoïds, not only on PQ, have also been observed. (Bornman et al., 1983) observed fusion of thylakoids and accumulation of starch which are symptoms associated with damage to thylakoids. (Mantai et al., 1970) had already attributed the inhibiting effect of UV-C light on photosynthesis to a disruption of