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UVB and UVA as eustressors in horticultural and agricultural crops

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ABSTRACT

The production of high quality fruits, vegetables and ornamental crops while employing natural processes to maintain plant productivity, is an overarching goal of sustainable horticulture and agriculture. The nutritional quality of people's diet is a key factor in the prevention of many chronic diseases, including obesity and heart disease. Traditionally viewed as detrimental to crops, recent evidence now shows that natural levels of ultraviolet radiation (UV; 280–400 nm) in sunlight can actually have a number of beneficial effects on the performance and nutritional quality of many fruits, vegetables and ornamental crops. UVB (280–315 nm) and UVA (315–400 nm) were shown to have effects on the growth, photosynthesis, secondary plant metabolites and the plant-insect interaction in important horticultural and agricultural crops. This review aims to summarize these effects. Compared to UVB, the number of studies on the effects of UVA is very limited mainly due to the experimental design that often does not allow studying the effect of UVA independent from the effect of UVB. Recently, LEDs offer the possibility to tailor the light spectrum which will open doors for the investigation of the effect of UVA and UVB and UVA/blue light photoreceptors. The production of flavonoids-a class of plant secondary metabolites that are known to have various health benefits, is well-known as a plants response to enhanced UVB radiation. Flavonoids serve multiple functions in plants (e.g. UV shielding or antioxidants) but species vary greatly in flavonoid profiles and responsiveness to UV. The contribution of other secondary plant metabolites is often neglected. However, these secondary plant metabolites affect plant quality such as aroma/smell, taste, color and compounds contribute to promote human health.

1. Introduction

Ultraviolet radiation (UV; 290–400 nm) comprises a relatively minor fraction of the total solar radiation reaching the earth's surface, yet radiation in this waveband is known to play an important role in regulating the growth and development of higher plants (Jansen and Bornman et al., 2012). Highly energetic shorter wavelengths of solar UV (UVB; 290–315 nm) can potentially induce a number of deleterious effects in plants, including disruption of the integrity and function of important macromolecules (DNA, proteins and lipids), oxidative damage, changes in plant biochemistry, partial inhibition of photosynthesis, and growth reduction (Jordan, 2002; Hideg et al., 2013; Albert et al., 2011). Consequently, UVB has traditionally been considered as stressor. However, recent studies have highlighted the regulatory properties of low, ecologically-relevant UVB levels that trigger distinct changes in the plant's secondary metabolism resulting in an accumulation in a structure-dependent accumulation of secondary plant compounds (Neugart et al., 2012b; Mewis et al., 2012; Schreiner et al., 2012). It turns out that plants have particular UV receptors that perceive UV radiation. The UVR8 receptor from *Arabidopsis thaliana* is specific to UVB (280–315 nm) radiation and leads to a signaling cascade via UVR8/COP1/HYH5/HYH (COP1, the multifunctional E3 ubiquitin ligase CONSTITUTIVELY PHOTOMORPHOGENIC 1; HYH5, ELONGATED HYPOCOTYL 5; HYH, HOMOLOG OF ELONGATED HYPOCOTYL; (Lang-Mladek et al., 2012) controlling a range of key elements for UVB acclimation (Brown et al., 2005). Also receptors such as cryptochroms, phototropins and Zeitlupe proteins exist that strongly absorb in the UVA (315–400 nm) part of the spectrum (Heijde and Ulm, 2012; Casal, 2013). To date, there is an enormous number of studies investigating the effect of UVB in plants. In contrast, UVA is seldom studied manly due to difficulties in the study design, even though the solar radiant energy contains 10–100 times more UVA than UVB photons (Verdaguer et al., 2017).

The acclimation to UV appears sufficient to largely minimize any detrimental effects of UVB on plant growth and productivity when plants are grown under ambient or realistically enhanced UVB in the field (Ballare et al., 2011) such that photomorphogenic (and often beneficial) effects of UV generally predominate under these conditions

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(Wargent and Jordan, 2013) smaller but thicker leafs, less plant height and lower biomass (Jansen et al., 1998; Caldwell et al., 1995; Barnes et al., 1988; Hofmann et al., 2000; Caldwell et al., 2007; Jansen and Bornman et al., 2012) or modified photosynthesis (Hideg et al., 2013; Kataria et al., 2014). One of the most important and widespread protective responses of plants to UV radiation involves the induction and synthesis of flavonoids and related phenolic compounds that function as UV shielding components and antioxidants (Agati et al., 2013; Caldwell et al., 1983). Flavonoid biosynthesis is influenced by UVB, UVA (315–400 nm) and visible radiation (400–700 nm; (Flint et al., 2004; Siipola et al., 2015) and appears to be mediated, at least in part, by the UVB photoreceptor UV RESISTANCE LOCUS 8 [UVR8] (Morales et al., 2013; Rizzini et al., 2011). The accumulation of flavonoids and related UV-absorbing compounds in epidermal tissue decreases epidermal UV transmittance (TUV) (Mazza et al., 2000; Bidel et al., 2007) and is a primary mechanism by which plants acclimate to changing UV environments, including alterations resulting from stratospheric ozone depletion and climate change (Bornman et al., 2015). The investigation of other secondary plant metabolites is rare but recent results show that UV also affects glucosinolates, carotenoids and other secondary plant metabolites (Schreiner et al., 2012).These changes in plant characteristics also affect plant quality and is of importance to meet the consumer preferences for fruit and vegetables as well as ornamental crops as this includes growth and development, aroma/smell, taste, color and compounds promoting plant and human health (Schreiner et al., 2013).

Most plants grown in greenhouses and plastic tunnels lack the adaptation to UV radiation during their growth. They consequently have lower concentrations of phenolic compounds (Wargent and Jordan, 2013) and the transfer of seedlings or young plant to the field causes sun burn especially caused by UVB. The reduction of UVB and UVA, and the regulatory effect of this UV reduction on the plant's growth and secondary metabolism results in higher growth, yield and photosynthetic pigments (chlorophylls and carotenoids) in monocots such as sorghum and wheat (Kataria and Guruprasad, 2015, 2012a). Also, in tomato fruits lycopene is increased in flesh and peel as consequence of UVB decrease (Lazzeri et al., 2012). In Brassicales species a structure-specific increase of flavonoid glycosides, but decrease of phenolic acids is found after UVB exclusion, while total UV exclusion including UVA and UVB led to low concentrations of flavonoid glycosides and phenolic acids (Reifenrath and Mueller, 2007; Morales et al., 2013). In contrast, traditional cultivation techniques increase sunlight and concomitantly UVB and UVA during plant growth and ripening e.g. the reduction of leaves in vine during berry ripening (Diago et al., 2012, 2009; Pastore et al., 2013) or the use of reflecting foils underneath apple trees (Jakopič et al., 2010). Even more common is the use of additional light, which is to date mainly high pressure sodium lamps, in greenhouses during the production of vegetables and mainly ornamental crops. Recently, LEDs (light emitting diodes) offer the possibility to tailor the light spectrum producers need to grow plants fast and with good quality by at the same time saving energy (van Ieperen, 2012; Taulavuori et al., 2013; Huché-Thélier et al., 2016). The use of LEDs for plant growth lighting or targeted triggering of certain plant properties is a new approach in the research of greenhouse production of horticulture crops and gained much interest the related industry (Olle and Virsilé, 2013). In contrast to the still less uses UVA und UVB LEDs, the most commonly used wave length are blue (450–495 nm), red (620–750 nm) and far-red (710–850 nm). Changes in blue light also control stem morphology, with blue light impeding stem elongation (Franklin and Whitelam, 2005). Blue light also has a decreasing effect on the biomass of lettuce and spinach (Ohashi-Kaneko et al., 2007) but increasing effects on plant secondary metabolite concentration such as caffeic acid derivatives, quercetin and kaempferol glycosides as well as anthocyanins (Taulavuori et al., 2016; Nascimento et al., 2013; Johkan et al., 2010; Siipola et al., 2015). In contrast red light is more widely known to increase elongation of shoot and petiole as a response of the plant to shading mediated by phytochromes (Franklin and Whitelam, 2005) and induce flowering but is not known to modify the secondary metabolism of plants (Demotes-Mainard et al., 2016). However, synergistic effects of blue and red light regarding plant growth and secondary metabolism are found (Johkan et al., 2010; Hogewoning et al., 2012; Kopsell et al., 2014).

Artificial light sources to increased UVB and UVA radiation is not yet often used in horticulture due to law restriction in food production (e.g. REGULATION (EC) No 178/2002 OF THE EUROPEAN PARLIAMENT AND OF THE COUNCIL of 28 January 2002 laying down the general principles and requirements of food law, establishing the European Food Safety Authority and laying down procedures in matters of food safety) and still high prices for UVB and UVA LEDs. However, UVB during plant growth leads to more compact and branched plants (Huché-Thélier et al., 2016) which oscillates with the consumer preferences for ornamental crops (Boumaza et al., 2010) and herbs. The same is true for vegetables as well as the before mentioned changes in the plant's metabolism that affects the plant quality (Schreiner et al., 2012; Jansen et al., 2008). Rapid advances in the development of UV-emitting LEDs will make it possible to add single UVB and UVA wavelengths to the light spectrum in greenhouses and are under investigation at the moment. This review aims to state the knowledge of UVB and UVA as eustressor and its effects on growth, photosynthesis, secondary plant metabolites and plant-insect interactions.

2. Growth

Plants respond to environmental changes by the adjustment of their morphology and growth (Fig. 1, Table S1). Part of it is suggested as the plant's action to avoid or increase shading conditions and optimize its functionality (Robson et al., 2015).

It has been shown in several experiments that UVB is negatively associated with biomass production in plants producing fruits and vegetables (Choudhary and Agrawal, 2014; Kuhlmann and Mueller, 2009; Guruprasad et al., 2007; Zhang et al., 2014; Agrawal and Mishra, 2009; Kumari et al., 2009; Nithia et al., 2005; Liu et al., 2013; Sangtarash et al., 2009; Baroniya et al., 2014; Gao et al., 2003; Yao et al., 2005; Antonelli et al., 1997; Ambasht and Agrawal, 2003; Tezuka et al., 1993) and in monocots (Gao et al., 2004; Yuan et al., 1998; Deckmyn and Impens, 1997; Häder, 1996) most of them are of enormous interest as agricultural crops. This consequently leads to losses in the product weight e.g. for lettuce (Paul et al., 2012) and monocots such as rice (Hidema et al., 2005) wheat (Kataria and Guruprasad, 2012b) or sorghum (Kataria and Guruprasad, 2012a). However, some studies report increased biomass with UVB (Singh et al., 2015; Yang and Yao, 2008; Liu et al., 1995; Sakalauskaitė et al., 2012; Rai et al., 2011) or no effects (Allen et al., 1999; Behn et al., 2011; Krizek et al., 1997; Lizana et al., 2009). The reason for this different results is mainly caused by the experimental design e.g. time of UVB treatment -shorter experiments often find no effect or positive effects on the biomass production-as well as UVB:PAR ratio- as higher photosynthetically active radiation (PAR) triggers plant protection and reduces the effect of UVB (Majer and Hideg, 2012b). There is a lack of knowledge on UV induced biomass changes in ornamental crops species as this is not the most important aspect for these plants. The leaf area is highly affected by UVB and mainly decreases with higher levels of UVB (Choudhary and Agrawal, 2014; Gao et al., 2003; Guruprasad et al., 2007; Zhang et al., 2014; Kataria et al., 2013; Yang and Yao, 2008; Yao et al., 2005; Singh et al., 2011; Baroniya et al., 2014; Deckmyn and Impens, 1997; Yuan et al., 2000; Kumari et al., 2009; Sakalauskaitė et al., 2012; Krizek et al., 1997; Häder, 1996; Antonelli et al., 1997; Sangtarash et al., 2009) e.g. by the reduction of the leaf length (Klem et al., 2012). Further processes affecting the leaf's architecture is a thicker epidermis and consequently thicker leaves (Rai et al., 2011; Pollastrini et al., 2011; Day and Vogelmann, 1995). A very obvious effect of UVB in plants is the reduction of plant height in vegetables and especially monocots (Kuhlmann and Mueller, 2009; Agrawal and Mishra, 2009; Gao et al.,

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