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**REVIEW ARTICLE**

# Cytoskeleton-mediated signalling pathways in UV-B perception by plant cell

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**Abstract**

Currently, the portion of ultraviolet B (UV-B) (280–315 nm) in total solar radiation reaching the earth's surface increases steadily revealing potentially adverse effects on terrestrial organisms. Plant morphological and functional responses induced by UV-B are principally described, however, the elucidation of downstream-effectors in UV-B-triggered pathways are still of particular interest, whereas they would allow to develop protective approaches aimed to increase multiple plants' tolerance to various abiotic stresses. The main focus of this review is on the contribution of cytoskeletal proteins into UV-B signalling in plants.

*Key words*: Plants, UV-B, Signalling, Cytoskeleton, Reactive oxygen species, Nitric oxide

## Introduction

Impacts of ultraviolet (UV, 200−400 nm) non-ionising radiation on living organisms became an important environmental issue over the past four decades since the first reports of climate and/or anthropogenic depletion of the protective stratospheric ozone layer have appeared (Ballarè et al., 2011; McKenzie et al., 2011). As UV irradiation is not photosynthetically active except a short range of UV-A waveband close to violet visible light, algae and higher plants are reluctant to counteract UV through the development of the protective mechanisms or to tolerate *via* the adaptation to UV during the process of their evolution (Holzinger and Lütz, 2006). The enhanced UV-B (280−315 nm) exposure of Earth surface reveals both a range of deleterious effects such as nucleic acids/proteins damage, alterations in photosynthesis, transpiration, growth and development, etc. (Rozema et al., 1997; Hollósy, 2002), though ambient doses of UV-B trigger adaptive morphogenic responses (for review see Jansen, 2002).

Since sessile plants are not able to respond to (a)biotic stress factors by "fight-or-flight-or-freeze" strategy as animals do, they have developed a highly branched stress signalling pathways. The finely tuned molecular net operating in plant cell in response to stress factors is not studied well, and little evidence is accumulated concerning the integrative molecules and convergent reactions in partially overlapping pathways. The starting point of UV-B signalling is UV-B sensing by the special photoreceptor that was originally identified as a regulatory protein for UV-B-triggered signal transduction (Jenkins, 2009; Rizini et al., 2011). Light perception is important for all life kingdoms, but for plants it is vital as a main energy source and photomorphogenic trigger. Specific families of photoreceptors allow plants to sense wide wavelength range of light (Jenkins and Brown, 2007; Wu et al., 2012). For instance, red/far red is perceived by phytochrome, UV-A – by phototropin and cryptochrome, and UV-B – by recently discovered UV RESISTANCE LOCUS8 (UVR8), broadly present, constitutively expressed and well-conserved among plants (Rizini et al., 2011; Wu et al., 2012). Upon UV-B exposure, both natural and simulated, UVR8 homodimer monomerizes and interacts with CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1) to relay the signal (Jenkins, 2009; Rizini et al., 2011; Wu et al., 2012).

For UV-B can evoke a generalized cellular response, information perceived by UVR8 and other putative receptors has to be transduced *via* the second messengers to the target molecules, either proteins or genes (Broschè and Strid, 2003; Frohnmeyer and Staiger, 2003; Ulm, 2006). Some of the UV-B-responsive genes encode proteins participating in DNA repair, photosynthesis, cell

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cycle regulation, biosynthesis of the protective pigments, as well as the antioxidant enzymes and other wound/defence proteins such as pathogenesis-related protein 1 (PR-1) (Hollósy, 2002; Broschè and Strid, 2003). UV-B response of plant cell also involves the reactive oxygen (ROS) and nitrogen species (RNS) formation, cytoplasmic $Ca^{2+}$ content increase, burst-like synthesis of such phytohormones as ethylene, abscisic, salicylic and jasmonic acids, ion channels and kinase/phosphatase cascades activation and other reactions (Fraire-Velázquez et al., 2011). ROS, mainly, $H_2O_2$, singlet oxygen, superoxide and hydroxyl radicals could play a role of key signalling molecules under UV-B stress (Mackerness et al., 1999, 2001). Besides that, UV-B-induced plant morphological responses are assumed to be realized by the direct or indirect NO signalling (Mackerness et al., 2001; Zhang et al., 2003; Krasylenko et al., 2012). In addition, UV-B has been proposed to stimulate the expression of plant-pathogen-interaction genes *via* the octadecanoid pathway related to wound signalling (Surplus et al., 1998).

Despite the fact that numerous publications are devoted to UV signalling in plants, possible involvement of plant cytoskeleton as a highly responsive UV target is poorly studied. Therefore, in this review the effects of UV-B irradiation on plant cytoskeleton are highlighted regardless the ecological relevancy of UV-B doses as the data about the UV-B impact on plant microtubules and microfilaments is scarce.

**Cytoskeleton as a common participant in responses of plant cell to environmental stimuli**

Cytoskeletal network of plant cell is formed by the integrated arrays of microtubules (MTs), actin filaments, intermediate filaments, microtubule- and actin-related proteins and others (Gardiner et al., 2011, 2012; Wasteneys and Yang, 2004). Plant cytoskeleton provides the realization of such basic processes as cell division, growth and development, membrane anchorage, cell shape support and communication, polymer cross-linking, vesicle transport, cyclosis, etc. (Foster et al., 2003; Wasteneys and Yang, 2004). Its dynamic instability is one of the mechanisms of adaptive rearrangements (Baluška et al., 2001) in response to such environmental stimuli as light (Lahav et al., 2004), gravity (Kordium et al., 2008), cold (Sheremet et al., 2012), heat (Hussey and Hawkins, 2001), touch and wind (Telewski, 2006). Phytohormones (Foster et al., 2003; Wasteneys and Yang, 2004; Bright et al., 2006; Blume et al., 2012), regulatory intracellular molecules − $Ca^{2+}$ (Lui et al., 2003), $H_2O_2$ **(**Bright et al., 2006), NO (Yemets et al., 2009, 2011), protein kinases and phosphatases (Yemets et al., 2008a,b; Blume et al., 2010) and many others control the organization and dynamic properties of cytoskeleton components, modulating thus the signal transduction cascades. Even more, it was postulated that the plant cytoskeleton is a major target of signalling events (Wasteneys, 2004). Multiple stress factors such as high salt (Wang et al., 2007), herbicides (Ovidi et al., 2001), and heavy/toxic metals content in soil (lithium (Bartolo and Carter, 1992), tungsten (Adamakis et al., 2010), lead (Liu et al., 2009), chromium (Eleftheriou et al., 2012) aluminium (Schwarzerovà et al., 2002), cadmium, nickel (Dovgalyuk et al., 2002) and others) as well as plant colonisation by viral, bacterial or fungal pathogens (Schmidt and Panstruga, 2007) also induce stress-responsive and/or adaptive MTs reorganization (Wasteneys and Yang, 2004).

As cytoskeleton orchestrates the important processes in plant cell listed above, and some of these basic processes are known to be affected by UV-B, we anticipate that cytoskeletal structures can be involved into intracellular UV-B signalling. Hence, tubulin in microtubules and/or actin in microfilaments as well as proteins of intermediate filaments may percept and transduce the signal from UV-B playing a role of UV-B downstream-effectors. However, both experimental design and target organisms are manifold and appreciably diverse, what makes the identification of these target molecules to be rather challenging task.

Numerous reports concerning the alterations of plant growth and morphology (root/shoot ratio and development reduction, lowered/increased rate of cell division, leaf thickening, cotyledon curling, axillary branching, increased flower number and diameter, etc.) as commonly observed responses to UV irradiation exist (Hollósy, 2002; Jansen et al., 2002; Ktitorova et al., 2006). For instance, the zygotes of *Fucus serratus* and *F. spiralis* subjected to UV-A revealed only the inhibition of cell division, though UV-B-irradiated zygotes remained spherical and could not divide, polarize and germinate to form rhizoides, what may be related to the cytoskeleton damage (Schoenwaelder et al., 2003). UV-B exposure in dose of 10.08 kJ $m^{-2}$ $d^{-1}$ inhibited cell division of wheat (*Triticum aestivum* L.) callus accompanied by different chromosomal aberrations such as micro- and multinuclei formation (Zhang et al., 2009) that also may be explained by the alteration of cytoskeleton organization, treadmilling and/or dynamic

instability. In leaves of pea (*Pisum sativum* L.), commelina (*Commelina communis* L.), and oilseed rape (*Brassica napus* L.) the enhanced (11−32 $kJ/m^{-2}d^{-1}$) UV-B exposure impaired the stomatal turgor and conductance, possibly, by changes in cell wall elasticity or, alternatively, by cytoskeleton reorganization in guard and neighbouring epidermal cells (Nogués et al., 1999).

In general, the underlying mechanisms of such UV-induced morphological changes remain poorly understood, and only a few articles are focused on the cytoskeleton rearrangement as one of the events highlighting UV-B-induced cellular responses in plants (Staxèn et al. 1993; Guo et al., 2010; Chen et al., 2011; Jacques et al., 2011; Krasylenko et al., 2012). Thus, the pioneer work investigated the direct effects of the enhanced UV-B (4–24 mmol photons/$m^2$) on *Petunia hybrida* mesophyll protoplasts that led to the reversible dose-dependent fragmentation of cortical MTs and to the inhibition of cell cycle progression in $G_1/S/G_2$ phases at 24 h after the irradiation (Staxèn et al., 1993). It has to be noted that at 72 h after the irradiation only in protoplasts exposed to 24 mmol photons/$m^2$ UV-B MTs were shorter than those of the non-irradiated protoplasts, while in other treatments MTs recovered their initial organization comparable to control (Staxèn et al. 1993). After the decade-long gap it was established that MTs in *T. aestivum* mesophyll protoplasts were depolymerized significantly to sticks and spots under the enhanced UV-B (10.08 $kJ \cdot m^{-2} \cdot d^{-1}$), and their fluorescence intensity decreased (Guo et al., 2010). The experiments of UV-B impacts on MTs using *gfp-map4* (*m*icrotubule-*a*ssosiated *p*rotein 4) expressed in *Arabidopsis thaliana* seedlings revealed that the UV-B exposure (13.6–68 $kJ/m^2$) randomize, depolymerize or/and stabilize both interphase and mitotic MTs in epidermal as well as in cortex cells of all primary root zones in dose-dependent manner (Krasylenko et al., 2012). For example, in 2 h after the 13.6 $kJ/m^2$ cortical MTs became randomized only in epidermal cells of the transition, elongation and partially differentiation zones as well as in epidermal cells of root tip. In 2 h after 27.2 and 34 $kJ/m^2$ UV-B exposure the randomization and/or fragmentation of MTs occurred not only in epidermal cells, but also in cortex cells of all root zones. The observed UV-B-induced MTs randomization is supposed to be the moving force of epidermal cell swelling and excessive root hairs formation. It was shown that the most sensitive to UV-B were cortical MTs in transition/elongation zones as they depolymerized immediately after the UV-B exposure (Krasylenko et al., 2012), what gives additional evidence that the transition zone is a signalling–response nexus in the root. In this zone the inputs from endogenous (hormonal) and exogenous (sensorial) stimuli are integrated and translated into signalling and motoric outputs as adaptive differential growth responses (Baluška et al., 2010). In details, transition zone cells are known to be sensitive to auxin, ethylene and extracellular $Ca^{2+}$ as endogenous factors as well as mechanical pressure, aluminum, and microorganisms as exogenous factors (Baluška et al., 2001). In turn, cortical MTs in epidermal cells of the transition zone are also exceptionally sensitive to fluctuations of auxins (Takahashi et al., 2003), NO content (Yemets et al., 2009, 2011), protein kinases/phosphatase inhibitors (Sheremet et al., 2010) and cold treatment (Sheremet et al., 2012).

Furthermore, in 6 h after UV-B irradiation (27.2 and 68 $kJ/m^2$) of control and *gfp-map4*-expressing *A. thaliana* seedlings, whose primary roots were covered with aluminum foil in order to protect them from the direct UV-B influence (shielded roots), dose-dependent MTs randomization, depolymerization or bundling in epidermal root cells of transition and elongation zones were established by laser scanning confocal microscopy. MTs organization in epidermal cells of above- and underground *A. thaliana* organs differed in sensitivity to UV-B. The most resistant were MTs in stomatal cells of adaxial leaf surface, and, in a lesser extent, in hypocotyls, as they were oriented radially after the UV-B exposure (Krasylenko et al., 2011). In stomatal cells of non-irradiated seedlings MTs were organized in radial net of toughly adjacent bundles (Shi et al., 2009). Less resistant in comparison to stomatal cells were MTs in leaf epidermal cells that were partially depolymerized after 27,2 $kJ/m^2$ and completely depolymerized after 68 $kJ/m^2$ UV-B exposure, while in non-irradiated roots MTs oriented uniformly randomly. In cells of non-irradiated abaxial side MTs organization remains unaltered similar to control (Krasylenko et al., 2011). Relative resistance of MTs in the aboveground organs epidermal cells as compared to root cells could be explained by the presence of photoprotection and photoreparation mechanisms (Jansen, 2002). It was shown recently by other authors that UV-B inhibited the growth of *A. thaliana* leaf plates without MTs reorganization in adaxial leaf surface epidermal cells (Hectors et al., 2010, Jacques et al., 2011). The difference of

these results from our data could be explained by that other authors chronically exposed the leaves of the mature two-weeks-old *A. thaliana* plants with the elaborated defense mechanisms to low UV-B for 20 days that induced accumulative effects.

It is well-known that under chronic stresses MTs are able to be adaptively rearranged and/or reorganized because of their dynamic instability and threadmiling (Wasteneys and Yang, 2004), as well as by α- and β-tubulin posttranslational modifications, for instance, phosphorylation, acetylation and tyrosination/detyrosination cycle that define MTs stability (Blume et al., 2007; Yemets et al., 2008a; Blume et al., 2010). This can be the reason, why MTs rearrangements could not be visualized under chronic UV-B exposure by doses close to natural ones. In turn, MTs in hypocotyls' epidermal cells were more perceptible to UV-B then MTs in leaf epidermal cells, as 27.2 and 68 kJ/m$^2$ UV-B exposure caused partial depolymerization of MTs in hypocotyls cells (Krasylenko et al., 2011). Indeed, the indirect UV-B impacts on MTs organization in shielded *A. thaliana* root cells is an issue of special interest, since cortical MTs in epidermal cells of transition zone were the most sensitive to indirect UV-B effects. In 2 h after the UV-B exposure they become randomized or depolymerized, while in the same cells of non-irradiated roots MTs were oriented transversely. In epidermal cells of elongation and differentiation zones MTs randomization in 2 h after the UV-B irradiation also occurred, while in root apex cells there were no MTs rearrangements (Krasylenko et al., 2011). These data give extra evidence to the existence of the stress signal transduction mechanism from the irradiated aboveground organs to non-irradiated underground ones *via* such long-distance secondary messengers as ROS and RNS that were proposed to be the important secondary messengers under UV-B stress in plants *in vitro* and *in vivo* (Mackerness et al., 2001; Zhang et al., 2003; An et al., 2005; Shi et al., 2005; Krasylenko et al., 2012). It is supposed that NO could be involved into MTs reorganization under UV-B influence, because exogenous NO donors and scavenger, as well as the modulator of its endogenous content cause MTs reorganization in epidermal cells of the sensitive transition and elongation zones of *A. thaliana* primary root cells (Yemets et al., 2009, 2011).

Moreover, UV-B-induced MTs reorganization in cells of shielded *A. thaliana* roots was accompanied by the alteration of MTs-related processes of growth and differentiation. Thus, the growth inhibition of shielded *A. thaliana* primary roots was not as significant as in non-shielded ones. In 24 h after the UV-B exposure, the successive epidermal cells swelling together with the intense root hairs formation in differentiation zone of shielded roots was revealed as compared to non-irradiated roots what points out to the activation of the morphogenetic processes. In UV-B-induced plant morphogenetic response and in the formation of the respective stress phenotype may participate phytohormones (especially, auxins and ethylene) and ROS (Potters et al., 2009). Since in UV-B-exposed plant cells ROS, RNS and NO are formed (Mackerness et al., 2001; Zhang et al., 2003), we could suggest the involvement of the latter into plant morphogenic responses induced by the UV-B. Taking into account that during oxidative stress endogenous NO content in plant cells was shown to increase under UV-B exposure (Mackerness et al., 2001; Zhang et al., 2003), the combined effects of NO-modulating chemicals and UV-B irradiation on MTs organization of were studied. The seedlings of *A. thaliana* (GFP-MAP4*)* were exposed to enhanced UV-B doses (6.8–68 kJ/m$^2$) with or without sodium nitroprusside (SNP) as exogenous NO donor, or 2-(4-carboxyphenyl-4,4,5,5-tetramethylimidazoline-1-1oxyl-3-oxide potassium salt (c-PTIO) as its specific scavenger pretreatment. In 24 h after UV-B irradiation SNP-pretreated *A. thaliana* seedlings partially recovered MTs organization in epidermal cells of elongation zone, whereas c-PTIO-pretreated ones have not markedly improved it in cells of the same root zone (Krasylenko et al., 2012). It was also shown that SNP pretreatment of UV-B irradiated *A. thaliana* seedlings rescued the UV-B-inhibited root growth in 48 h as distinct from c-PTIO pretreatment (Krasylenko et al., 2012). Furthermore, SNP also partially recovered UV-B-altered primary root morphology and returned UV-B-disturbed MTs organization to the initial one in epidermal cells of *A. thaliana* root cells on the contrary to c-PTIO pretreatment. Hence, NO donor protects microtubule organization as well as MT-mediated root growth and development from the disrupting UV-B effects that corroborate the results of other authors (An et al., 2005; Shi et al., 2005). As MTs organization in *Arabidopsis* root cells depends on NO content under the enhanced UV-B exposure, we suppose that microtubules can be components of NO-mediated signalling cascades induced by UV-B stress.

Cytoskeletal reorganization along with DNA phototransformation, membranes and cell morphology alterations is considered to be the key hallmark of UV-induced apoptosis in mammalian

cells (Ndozangue-Touriguine et al., 2008). Nevertheless, the involvement of both MTs and microfilaments (MFs) in programmed cell death in plant cells is still unknown. To study the role of MTs and MFs in cell death, the suitable model for *in vitro* vital cytoskeleton visualization − the cells of *Nicotiana tabacum* Bright Yellow-2 (BY-2) suspension culture expressing *gfp-mbd* (*m*icrotubule-*b*inding *d*omain of MAP4) was chosen. As BY-2 cells are highly resistant to the enhanced UV-B, the doses of 34, 81 and 135 kJ/m$^2$ were (SNP) as used (Lytvyn et al., 2010). Dose-dependent depolymerisation of both interphase and mitotic microtubules occurred in 3 h after the exposure together with the cytoplasm shrinkage and chromatin condensation (Lytvyn et al., 2011). However, MTs were only randomized in cells that have not undergone apoptosis, as in 3 h after 81 and 135 kJ/m$^2$ UV-B exposure the apoptotic cells percentage was 23.8% and 29 %, respectively (Lytvyn et al., 2010). MTs depolymerization was also accompanied by micronuclei formation and cytoplasm vacuolization (Lytvyn et al., 2011).

The main finding in these experiments is the clear correspondence of MTs depolymerisation and cytoplasm shrinkage that could point out at MTs involvement in the mediation of the apoptotic cytoplasm retraction in the UV-B-irradiated plant cells. Plant mictotubular cytoskeleton is also regulated by UV-B on genetic level, since rapid transcriptome responses of maize (*Zea mays* L.) occurred in irradiated and shielded tissues, and 11 cytoskeleton genes including α- and β-tubulin 1 as well as actin 4 were downregulated (Casati and Walbot, 2003).

The organization of other plant cytoskeleton component, such as F-actin filaments, was disturbed in interphase cells of wheat root-tip under the enhanced UV-B (10.08 kJ·m$^{-2}$·d$^{-1}$) (Chen et al., 2011). The F-actin arrays disintegrated into randomized short fragments during prophase, and totally disappeared in meta-, ana- and telophases that was accompanied by such chromosome aberrations as logging, bridges formation and partition-bundle division (Chen et al., 2011).

## Conclusions

The data presented here show that the cytoskeleton components could be implemented in UV-B signalling pathways, since both microtubules and microfilaments respond to this abiotic factor in dose-dependent manner either by the reorientation or by the reorganization (randomization, fragmentation or depolymerization). The paradigm shift in relation of cytoskeleton role in cell biology has been occurred recently. For a long time, it has been supposed to play a role of eukaryotic cellular "scaffolding", however, actually, the cytoskeletal proteins are the key participants in many signalling events.

In general, the identification of the cytoskeletal players in intracellular UV-B signalling cascades and the ways they cross-link in plant cell are very promising for the development of the protective approaches aimed to enhance plant tolerance to persistently pressing abiotic stress factors.

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