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Review

The role of UV-B radiation in plant sexual reproduction

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ABSTRACT

UV-B radiation affects plant sexual reproduction, but, at present, general patterns about the nature of these effects and their underlying mechanisms remain elusive. In recent years, plant UV-B research has experienced a substantial conceptual change, from a stress-dominated view towards a more regulatory perspective. With this in mind, we have surveyed the published literature on the effects of UV-B radiation on plant reproductive traits and on plant–pollinator interactions.

Most floral parts are effectively UV-B protected thanks to the accumulation of UV-B absorbing compounds. However, the least protected parts, such as pollen, are sensitive to high UV-B doses. Among UV-B absorbing compounds, flavonoids have a complex role in plant reproduction, since they are essential for UV-B protection and normal pollen function, while they also modulate flower and fruit colouration, which, in turn, affects visits by pollinators and frugivores. Effects of UV-B radiation on pollination can be direct, due to UV-B effects on pollinators, or indirect, due to pollinators responding to UV-B-mediated changes in plants. In the case of annual species, our literature survey revealed that, as UV-B doses increase, there is a tendency to delay the onset of flowering and to decrease fruit and/or seed production. Yet, the present review highlights the existence of complex dose–response curves that emphasize the need to use multiple UV-B doses in future studies of UV-B-mediated flowering responses. Moreover, species, populations or even cultivars originating from geographical areas with high impact of solar radiation (*e.g.* Mediterranean Basin) exhibit, in general, high protection against UV-B radiation, often showing positive responses to moderate UV-B increases.

In conclusion, our survey of the literature reveals complex UV-B effects on plant reproduction. To fully comprehend these effects, integrated approaches, beyond those currently used, are required to analyze the complex mixture of direct and indirect, stimulatory and inhibitory UV-B responses.

Contents

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Introduction

UV-B photons can have substantial biological effects on living organisms. Plants, in particular, are exposed to UV-B radiation (280–315 nm) due to their photosynthetic life-style. High doses of UV-B radiation have been widely reported to cause plant stress, leading to reduced biomass accumulation, DNA-damage, photosynthetic impairment and lipid peroxidation (Jansen et al., 1998; Ballaré et al., 2011), although most of these studies have been focused on plant vegetative tissues. Far fewer studies have analyzed the effects of UV-B levels on plant reproductive tissues, but some of the studies that did so reported increases in plant reproductive biomass (*e.g.* flowering) in response to high UV-B levels (Day and Demchik, 1996b; Björn et al., 1997; Musil et al., 1999). Such increase in plant reproductive biomass has been interpreted as an emergency response, a generic strategy to accelerate reproductive output before the plant succumbs to the stressor (Wada and Takeno, 2010).

Conversely, many recent studies have shown that plants exposed to ambient or near-ambient UV-B levels are rarely stressed, thanks to a range of constitutive and inducible protective traits, including enhanced UV-screening, and the activation of antioxidant defences and/or photorepair (*e.g.* Hideg et al., 2013). This regulatory phenomenon whereby plants adjust their metabolism in response to a low level of stress is sometimes referred to as "good stress" or eustress (Hideg et al., 2013). Alternatively, these responses may also be referred to as simply "regulatory" (*i.e.* omitting any reference to stress), in analogy with other photoreceptor-mediated responses. On the contrary, a scenario whereby negative effects dominate (*e.g.* decreased biomass production, impaired photosynthesis and macroscopic damage) is referred to as distress (Hideg et al., 2013), or simply stress. Either way, it is clear that in recent years plant UV-B research has experienced a major paradigm shift with the focus moving away from stress to UV-B specific regulatory events (Jenkins, 2009).

It is known that plants raised under low UV-B display complex, acclimative changes in profiles of flavonoids and other metabolites, as well as in plant morphology including the structure of the inflorescence (Ballaré et al., 2011). A specific UV-B photoreceptor, UV RESISTANCE LOCUS 8 (UVR8), has recently been identified (Rizzini et al., 2011). The UVR8 protein interacts in a strictly UV-B dependent manner with the ubiquitin ligase CONSTITUTIVELY PHOTOMORPHOGENIC (COP1) (Favory et al., 2009), controlling expression of genes associated with photorepair, antioxidant defence and accumulation of phenolic pigments (Jenkins, 2009; Heijde and Ulm, 2012). COP1 itself has also been associated with regulation of flowering (Liu et al., 2008; Favory et al., 2009). However, many of the UV-B-induced genes appear to serve primarily for UV-B protection, and effects on reproduction are likely to be indirect.

UV-B radiation can, thus, exert mechanistically distinct effects on plants depending on the UV-B dose (Fig. 1). High UV-B doses can cause oxidative stress, and under these conditions generic stress-induced flowering may also be anticipated (Wada and Takeno, 2010). Conversely, under low UV-B doses distress will be absent and UV-B-mediated flowering will be part of a specific, regulated process. Nevertheless, it is overly simplistic to interpret these as mutually exclusive responses. For example, even distress-inducing high UV-B levels will trigger signalling responses that contribute to acclimation and plant survival (Hideg et al., 2013). Consistent with this, the dose–response of UV-B mediated flowering is complex. Brodführer (1955) observed that lowering the UV-B dose (from 100% to 33% of ambient solar UV-B) stimulated development of a more branched inflorescence with more seed pods in *Arabidopsis thaliana* grown outdoors. Yet, lower UV-B doses (2% of ambient solar UV-B) decreased the same parameters. Such apparent disparities in UV-B response are commonly observed.

Apart from complex dose–response curves, it has long been known that UV-B responses depend on exposure conditions including the specific UV-wavelengths, PAR background levels, and other environmental factors. Genetic factors also play an important role in determining effects of UV-B on plant sexual reproduction (*i.e.* compare Petropoulou et al. (2001) and Koti et al. (2005)). Given the large number of interfering environmental parameters, it is not surprising that there is currently no consensus concerning the impact of UV-B radiation on plant reproduction. Moreover, the ecologically important process of plant reproduction frequently requires services of pollinators and frugivores. These species can be affected by plant responses to UV-B, but may also display their own specific UV-B responses, thus creating a further layer of complexity (Fig. 1). In this review we will analyze the literature on plant reproductive processes, bringing together disparate lines of research, in order to untangle UV-B-induced stress from UV-B-induced regulatory plant responses, as well as direct from indirect UV-B effects on plant sexual reproduction. The analysis presented in this manuscript will form the basis for an improved mechanistic understanding of the complex role of UV-B radiation in plant sexual reproduction.

Protection of floral structures against UV-B radiation

It has long been known that UV-B radiation can be an important stressor of plant tissues and organs (*e.g.* Jansen et al., 1998). Given that, in many species, flowers are placed in a position where exposure to UV-B is likely, the question that arises is how floral structures protect themselves from UV-B-induced stress. It is well known that one of the most effective defensive mechanisms against UV-B radiation in higher plants is the accumulation of a diverse range of phenolic metabolites (*e.g.* Tegelberg et al., 2001; Mpoloka, 2008; Nybakken et al., 2012). UV-B-induced phenolics, especially phenylpropanoids (*e.g.* cinnamic acid derivatives and flavonoids) occur in high concentrations in floral parts, such as sepals, ovaries and petals (Day and Demchik, 1996a). Among floral structures, ovaries seem to be better protected against UV-B radiation than other floral tissues as a result of having constitutively higher concentrations of UV-B protecting compounds (Day and Demchik, 1996a). On the other hand, many studies indicate that pollen is the most UV-B sensitive reproductive tissue, especially during anther dehiscence and pollen tube penetration into the stigma (*e.g.* Flint and Caldwell, 1984; Midgley et al., 1998; Torabinejad et al., 1998; Feng et al., 2000; Wang et al., 2010). Recently, Zhang et al. (2014) showed that in entomophilous alpine plants pollen grains normally protected by flower structures (such as bracts or petals) were more sensitive to UV-B radiation once removed from such structures than pollen grains originating in UV-B-exposed anthers. Accordingly, they suggested that pollen from entomophilous plants would be