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# Development-dependent effects of UV radiation exposure on broccoli plants and interactions with herbivorous insects

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ABSTRACT

The responses of plants to stress can highly depend on their developmental stage and furthermore influence biotic interactions. Effects of outdoor exposure to different ambient radiation conditions including (+UV) or excluding (−UV) solar ultraviolet radiation were investigated in broccoli plants (*Brassica oleracea* L. convar. *botrytis*) at two developmental stages. Plants either germinated directly under these different outdoor UV conditions, or were first kept for three weeks in a climate chamber under low radiation before outside exposure at +UV and −UV. Access of herbivores to the plants was possible under the outdoor conditions. Plants of both groups protected their tissue against destructive UV by increasing concentrations of phenolic compounds (flavonoids and hydroxycinnamic acids) after +UV exposure. But only plants that germinated under +UV conditions kept smaller than plants grown under −UV conditions, indicating certain costs for production of phenolics or for other potential metabolic processes specifically in young, growing plants. In contrast, growth of plants transferred at a later stage did not differ under both UV conditions. Thus, plants responded much more sensitive to the environment they experienced at first growth. Glucosinolates, the characteristic secondary compounds of Brassicaceae, as well as proteinase inhibitors, remained unaffected by UV in all plants, demonstrating independent regulation pathways for different metabolites. Plant infestation by phloem-feeding insects, Aleyrodidae and Aphididae, was more pronounced on +UV exposed plants, whereas cell content feeders, like Thripidae were more abundant on plants under the −UV condition. Choice experiments with the cabbage whitefly *Aleyrodes proletella* L. (Aleyrodidae), commonly found on *Brassica* spp., revealed that the key environmental cue navigating their behaviour seems to be the radiation composition, rather than plant quality itself. In conclusion, stress mediated changes of plant chemistry and morphology depend on the plant life cycle stage and are not necessarily mirrored in the behavioural responses of herbivorous insects.


## 1. Introduction

Plants are exposed to various abiotic and biotic stress factors throughout their life time. As organisms with a high phenotypic plasticity, they can adapt to changing environmental natural and agricultural conditions by different morphological, physiological and biochemical means (Lichtenthaler, 1998; Walling, 2000; Díaz et al., 2007). Thereby, the responses will depend on the developmental stage of the individual plant. The particular plant traits can influence in turn the attractiveness and susceptibility of the plants to herbivorous insects (Lavola et al., 1998; Zavala et al., 2001; Rousseaux et al., 2004).

Solar ultraviolet (UV) radiation is a highly dynamic abiotic environmental factor of major importance, which serves as an essential cue for growth and differentiation processes in plants. UV-B (280–315 nm) is the most energetic radiation reaching the earth's surface (Paul and Gwynn-Jones, 2003). When plants are not acclimatised or are irradiated with UV-B levels above the current ambient radiation, this radiation can have detrimental effects on lipids, proteins and nucleic acids, and specifically affect the photosystem II by damaging its membranes and decreasing enzyme activities (Rozema et al., 1997; Kolb et al., 2001; Bassman, 2004). UV-B leads also to an inhibition of cell expansion by reducing levels of indole-3-acetic acid (IAA), thereby affecting plant morphology (Rozema et al., 1997; Jansen et al., 1998). Plants have evolved various ways to cope with UV-B radiation, mainly by incorporating UV-absorbing flavonoids and hydroxycinnamic acids in the epidermis (Caldwell et al., 1983; Kolb et al., 2001). These phenolic compounds shield the photosystem against harmful radiation, serve as antioxidants, and change the optical properties of the plant (Treutter, 2005; Pfündel et al., 2006). They are also known to be involved in defence against herbivorous insects and pathogens (Treutter, 2005; Caputo

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et al., 2006) and UV-induced changes in plant chemistry can even effect members of the third trophic level, such as parasitoids (Foggo et al., 2007). Less is known about effects of UV-A (315–400 nm), however, also UV-A can induce the production of phenolics (Krizek et al., 1997, 1998). In general, signalling hormones are involved in the stress responses to UV. These hormones can mediate various other plant growth and defence responses (Mackerness, 2000; Stratmann, 2003). Furthermore, stress responses of plants to UV and herbivory overlap in gene expression. However, plants are also able to react in a stress-specific way (Mackerness, 2000; Stratmann, 2003; Pandey and Baldwin, 2008).

Different approaches were followed to test responses of plants to changed UV radiation regimes under controlled conditions. Effects of increased UV radiation were tested by using UV-lamps either in climate chambers (Lindroth et al., 2000; Tegelberg and Julkunen-Tiitto, 2001; Hofmann et al., 2003), greenhouses (Lavola et al., 1998; Wang et al., 2007) or under field conditions (Björn et al., 1997; Veteli et al., 2003). However, in these experimental set-ups partly unrealistic relative and absolute levels of photosynthetically active radiation (PAR, 400–700 nm) and UV radiation might be obtained (Rozema et al., 1997). In another approach, plants can be exposed to ambient outdoor radiation levels from which selectively predetermined wavelengths of the sunlight are excluded by the use of filter material (Hunt and McNeil, 1999; Mazza et al., 1999a; Kolb et al., 2001; Caputo et al., 2006; Reifenrath and Müller, 2007). With such filters plant responses can be tested under more ecophysiologically relevant conditions.

The formative imprint of an environmental cue highly depends on the stage of the plant life cycle and on the species to which the stress is applied, as well as on the duration of the treatment (Grammatikopoulos et al., 1998; Mazza et al., 1999a; Sultan, 2000; Reifenrath and Müller, 2007). Plants usually face a trade-off for resource allocation either to growth or to defence (Matyssek et al., 2005). However, this trade-off might differ in its extent for a young, developing *versus* a mature plant. A germinating plant has to build up an efficient protection system against abiotic and biotic harms rather rapidly to be able to produce photosynthetically active tissue for maturation. Thereby, a seedling or young plant might be exposed to a much stronger trade-off. For a mature plant, the resource distribution might be more flexible because of its stock of reserves. As it possesses already a substantial amount of photosynthetic active tissue, a mature plant might be able to invest more in the induction of chemical defence without measurable consequences in tissue growth.

A lot of domesticated crop plants like broccoli (*Brassica oleracea* L. convar. *botrytis*, Brassicaceae) are grown from seeds under attenuated ambient radiation conditions in greenhouses and are planted outside at an age of two to three weeks. In the field they have to adapt to the ambient radiation, and they have to cope and interact with various herbivorous insect species. Host plant quality is an important parameter that affects the performance of herbivorous insects (Awmack and Leather, 2002). Several insects are able to detect qualitative differences between individual plants and respond to different combinations of secondary metabolites in plants rather specifically (e.g., Reifenrath and Müller, 2008). But host plant chemistry is not the only information that triggers host choice behaviour of insects. For example, Mazza et al. (2002) demonstrated that thrips can perceive ambient UV-B radiation and prefer environments with low UV-B levels. Thus, visual cues are also of high importance for host seeking insects.

The aim of this study was to investigate the effects of different environmental irradiation conditions on growth and physical and chemical characteristics of broccoli in dependence of the plants' developmental stage and to measure the impact on natural insect infestation in a comprehensive approach. Cabbage whiteflies (*Aleyrodes proletella*, Aleyrodidae) were used as model to examine the cues navigating their behaviour in relation to the experimental design, as they were commonly found on the broccoli plants.

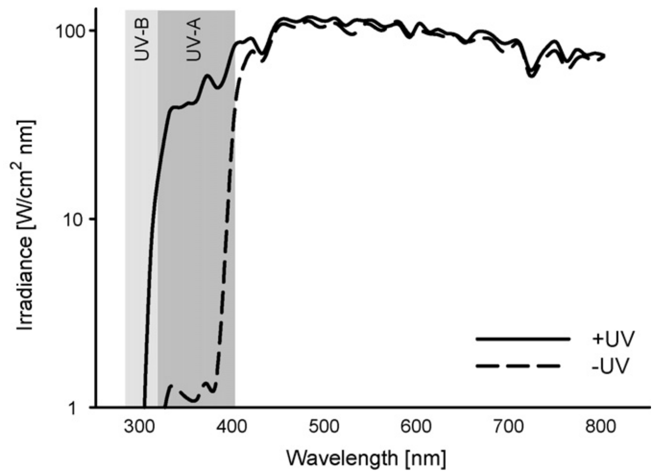


**Fig. 1.** Spectral irradiances under the filters (+UV: teflon foil, solid line; −UV: Lee 226 foil, dashed line) used in the experiments. Measurements took place in the early afternoon under cloudless sky. Areas of UV-B (280–315 nm) and UV-A (315–400 nm) wavelengths are highlighted in grey scales. Note the logarithmic *y*-axis.

## 2. Methods and materials

### 2.1. Plant material and growth conditions

Broccoli plants [*B. oleracea* L. convar. *botrytis* (L.) Alef. var. *cymosa* Duch. Monopoly; F1 Hybrid; Syngenta Enkhuizen, Netherlands] were grown from seeds in fertilised soil (ED 73, pH 6) in individual pots (diameter: 12 cm, height: 9 cm). Plants used for the "*late stress experiment*" (see below) were first kept in a climate chamber (20 °C, 16:8 h L:D, 70% r.h.) and after three weeks transferred outdoors in two types of filter tents including or excluding ultraviolet radiation (see below). Irradiance spectra in the climate chamber lacked UV-B, while low levels of UV-A were detected with 8 W/m$^2$. PAR was 371 $\mu$mol m$^{-2}$ s$^{-1}$. Irradiance spectra were measured with a X1$_2$ Optometer (Gigahertz Optik, Puchheim, Germany). Pots with seeds used for the "*early stress experiment*" (see below) were placed directly outside in the filter tents (ambient climatic conditions: temperature 6–30 °C, humidity 40–98%, 12:12 h L:D, mostly cloudless sky).

For plant exposure, 12 filter tents were built outdoors in the Botanical Garden of Würzburg directly before the start of the experiments. Spectrometer measurements (UNICAM UV4, ATI Unicam) of the filters were conducted regularly to control for alterations in filter transmission (Winter and Rostás, 2008). Tents consisted of wooden frames (1.20 m × 1 m ground area, 2.5 cm beam width) with the longer axis aligned in an east–west direction. The roof sloped from 1.3 m (north) to 0.9 m (south) height. Roofs and walls were covered with foil filters, except the northern wall. This wall was kept open to allow air circulation and insect entrance. At the roof and at the east and west side, the filter material overlapped the wooden frames for 10 cm. Plants were positioned close to the southern front in the tents, to limit the level of scattered radiation reaching the plants. Pots were placed in a distance of approximately 10 cm from each other. Six tents were covered by a teflon foil (Nowofol, Siegsdorf, Germany) transmitting the complete visible light spectrum and the ambient ultraviolet radiation ("+UV") (Fig. 1). The six other tents were covered by a Lee 226 UV foil (FFL-Rieger, Munich, Germany), which transmitted the complete visible light but filtered the entire UV-B range and most of UV-A ("−UV") (Fig. 1). Radiation-measurements were conducted in the