

Ultraviolet-B (UV-B) Radiation Effects on Plants[©]

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INTRODUCTION

The visible spectrum of light (400–700 nm) provides energy for photosynthesis and also information for plant growth and development through photoreceptor molecules (Briggs et al., 2001; Jordan et al., 1986; Nagy and Schäfer, 2002; Short and Briggs, 1994). At shorter wavelengths than the visible spectra is the ultraviolet (UV) region. This region is divided into three wavebands: UV-A (320–380 nm), UV-B (280–320 nm) and UV-C (< 280 nm). The passage of UV-A radiation is not restricted by stratospheric ozone and therefore passes through to the earth's surface. UV-C is lethal to biological systems and completely removed by the ozone layer. UV-B radiation, however, is removed to some extent by the ozone layer, but recent depletion in stratospheric ozone is allowing an increase in UV-B to impact on the biosphere. It is the increase in UV-B that is of concern to agriculture, horticulture, and ecosystems. This increase in UV-B has the potential to damage plants, change the development, and alter the chemical composition of plant tissue. In consequence, plant propagation under controlled environments must also take into consideration the quality of light including UV-B. For comprehensive reviews of UV-B effects on plants refer to Jordan, 1996; Jordan, 2002; and Campbell et al., 1999.

OVERVIEW OF UV-B EFFECTS ON PLANTS

Plants, because of their sessile nature, are particularly exposed to UV-B radiation and a wide range of effects has been described (Table 1). UV-B is absorbed by many important biological compounds including proteins, lipids, and nucleic acids (DNA and RNA). This absorption has potential to damage the plant, particularly by causing lesions in the DNA and consequently affecting gene activity. Plants however, seem to be very varied in their response to UV-B and a number of factors influence the response (Tables 1 and 2). Thus, UV-B effects on plants vary between species and even between varieties of the same species. Symptoms include changes in mor-

Table 1. Effects of UV-B on plants.

Changes in gene expression.
Decrease in photosynthetic activity.
Changes in protective pigment composition.
Changes in phytohormone production and transport.
Effects upon plant development and morphology.
Effects vary between species and within varieties of the same species.
Potential impact on the competitive ecology between plant species and with other organisms.

Table 2. Factors affecting UV-B induced responses.

Perception of the light environment.
Penetration of UV-B into the tissue.
Developmental stage.
Interaction with other environmental parameters.

phology (plant height, leaf area, etc), bronzing of leaves, silvery glazing, and desiccation of the tissue. Some plants even seem to undergo accelerated senescence after UV-B exposure. Other plants given exactly the same UV-B exposure will show no effects. Many factors seem to influence the UV-B induced response (Table 2), most notably other environmental parameters (e.g., light, heat, drought, etc.). A particularly important factor is the level of visible radiation present during the UV-B exposure. Thus high light seems to ameliorate the damaging consequences of UV-B. The mechanism is not fully understood, but this is a very common finding and particularly relevant to controlled-environment situations when the intensity of visible radiation is frequently low. In many studies of UV-B effects on plants low levels of visible radiation are combined with high levels of UV-B radiation, frequently resulting in exaggerated UV-B responses. The response to UV-B is also determined by the developmental stage of the tissue. Young tissue seems to be less susceptible to damage than older tissue. The timing of flowering may also be influenced, but this aspect of UV-B-induced responses has not yet been extensively investigated.

Plants defend themselves against UV-B in a number of ways. These defence responses are similar in some respects to those found in response to pathogens or herbivory. The three major defence mechanisms are:

- 1) Synthesis of protective pigments
- 2) DNA repair
- 3) Antioxidant production

Reflectance of UV-B at the leaf surface plays only a limited role in plant protection against UV-B. The "first line" of defence is due to pigments in the vacuoles of the epidermal cells. The pigments are water-soluble phenylpropanoid compounds that absorb in the UV region. The two main phenylpropanoid classes related to UV-B protection in plants are hydroxycinnamic acid conjugates and flavonoid glycosides (Schmitz-Hoerner and Weissenböck, 2003; Hofmann et al., 2000). Penetration of UV-B into lower cell layers does appear to take place through the cell walls between the epidermal cells (anticlinal walls). Levels of UV-B penetration vary substantially and this may well reflect how tolerant or susceptible a particular plant variety is. The second line of defence is within the cells and involves repair of damaged DNA and production of antioxidants to prevent oxidative damage induced by UV-B. Although DNA damage does take place, the repair enzymes are very effective and maintain a low level of lesions. An enzyme activated by light called photolyase seems very important in this role. Most importantly, UV-B light does not need to impinge directly on DNA to change the gene activity. It is now known that UV-B causes differential activation of gene activity. Genes that are involved in photosynthesis and metabolism tend to be switched off. Genes that produce protective pigments, antioxidants, etc. are switched on, i.e., taking part in the defence response. UV-B seems to work through intermediary chemicals that act as signals to cause a change in gene activity.

UV-B perception \Rightarrow Chemical signal \Rightarrow Change in gene activity

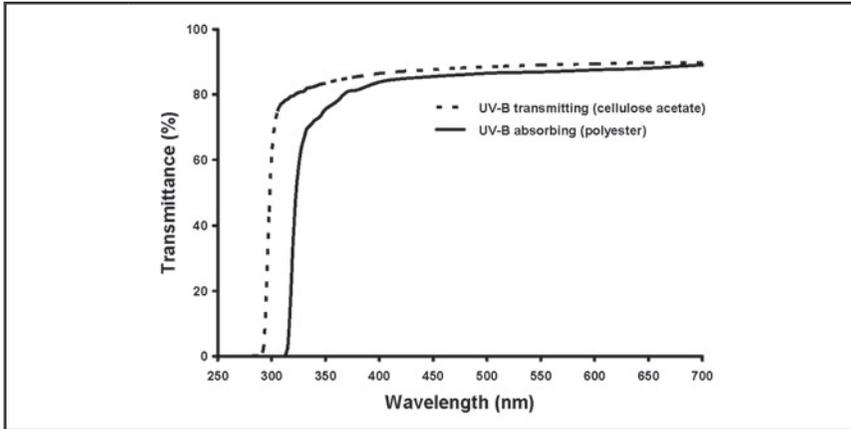


Figure 1. Comparison of UV-B-transmitting cellulose acetate with UV-B-absorbing polyester.

Table 3: Ultraviolet-B transmission and absorption of various materials used in UV filtration research. Typical thickness for these materials is 0.02 – 0.2 mm, except for window glass and polyacrylate Plexiglas (3 – 5 mm).

Filter	Transmits	Absorbs
UV-B-Transmitting		
Cellulose acetate	UV-A, UV-B	
Polychlorotrifluoroethylene (PCTFE)	UV-A, UV-B	
Fluoropolymer film (Tefzel [®])	UV-A, UV-B	
Copolymer of tetrafluoroethylene and hexafluoropropylene	UV-A, UV-B	
UV-B-transmitting polyacrylate	UV-A, UV-B	
UV-B-Absorbing		
Mylar-polyester	Most UV-A	UV-B
Other polyester	Most UV-A	UV-B
Polythene greenhouse film	Long-wave UV-A	Short-wave UV-A, UV-B
Window glass	Long-wave UV-A	Short-wave UV-A UV-B
LLumar [®] (CPFilms Inc., USA)		UV-A, UV-B
Polycarbonate (Lexan [®])		UV-A, UV-B

Lexan[®] GE Plastics, Pittsfield, Massachusetts, U.S.A.

Tefzel[®] DuPont Co. Wilmington, Delaware, U.S.A.

Table 4. Summary of UV-B responses

Extensive investigation of UV-B responses.
Lamp studies vs. UV-B filtration can show different levels of response.
Differential response of plants to UV-B.
Many responses overstated due to extreme experimental conditions.
Plants grown in reduced UV-B environments differ markedly from those grown under ambient UV-B.
Plant UV-B defence mechanisms are very effective.
Responses to UV-B are subtle and could have long-term consequences.
Very important interaction with other environmental conditions.

Any biosynthetic change will lead to a variation in the chemical composition of the plant. UV-B exposure may change the composition of a food product or the quality of the product due to modified external appearance. These changes may therefore impact upon commercial production of plants and products from them.

MODIFICATION OF UV-B EXPOSURE

A number of recent studies have used filters to investigate effects of reduced UV-B levels on plants. In contrast to studies with lamps, UV-B filtration studies use natural solar radiation as the source of UV-B. The majority of these studies compare UV-B-transparent with UV-B-opaque (but UV-A-transmitting) materials (Table 3). The latter mainly comprises polyester foils, while cellulose acetate is the most commonly used UV-B-transmitting material (Fig. 1). Tetrafluoroethylene and hexafluoropropylene copolymer (Teflon[®], DuPont Co. Wilmington, Delaware, U.S.A.) or polychlorotrifluoroethylene (PCTFE) (Aclar[®], Honeywell Inc., Morristown, New Jersey, U.S.A.) (Table 3) have been recommended as alternatives to cellulose acetate due to concerns about possible phytotoxic effects (Krizek and Mirecki, 2004). Ultraviolet-B-transmitting polyacrylate (Plexiglas[®], Atoglas division of Atofina Chemicals, Paris, France) is available where more robust cladding is required.

Ultraviolet-B filtration studies often reveal UV-B effects that are more pronounced than in studies supplementing UV-B with lamps. One factor explaining this is the fact that the ratio of ambient UV-B to exclusion UV-B in filter studies is usually much higher than the ratio of supplemental UV-B to ambient UV-B in lamp studies. Moreover, plants have developed a number of defence strategies against solar UV-B, as outlined above. Due to this defence, further increases of UV-B on top of ambient levels appear less effective than complete or near-complete UV-B exclusion.

Most importantly, the UV-B filtration research shows that natural, ambient solar UV-B represents a limiting factor for plant growth and development. Plants reared under UV-B exclusion often have higher biomass production, larger and thinner leaves, but also reduced levels of pigments and of secondary compounds which could affect plant colour, palatability, or taste (Krizek et al., 1998; Xiong and Day, 2001).

Thus, plants grown in a UV-B-free environment often display markedly different characteristics to those grown at ambient UV-B levels. Such differences need to be taken into account when propagating plants in indoor environments or glasshouses. Glasshouse cladding materials and window glass commonly do not transmit UV-B

and often also absorb various portions of the UV-A spectrum (Table 3). Ultraviolet-A has been shown to influence plant processes and can ameliorate UV-B damage (Caldwell et al, 1994; Krizek et al., 1998; Paul and Gwynn-Jones, 2003). To investigate UV-A effects, and to contrast these against UV-B effects, some studies have therefore included filters that absorb UV-B and UV-A (Table 3) (e.g., Krizek et al, 1998).

CONCLUSION

Overall UV-B effects on plants have been studied extensively, however, many results have been obtained under severe experimental conditions. Despite this problem a number of UV-B induced characteristics are clear (Table 4). It is now important to translate molecular and biochemical knowledge into potential impacts on agriculture and natural ecosystems.

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