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Effects of UV radiation and air humidity on morphology, stomatal function and photosynthesis of *Euphorbia pulcherrima*

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Abstract

The combined effects of relative air humidity (RH) and UV radiation were tested on three cultivars of *Euphorbia pulcherrima* (Willd ex. Klotzch) at different ontogenetic stages in controlled environment growth chambers. In addition, the effects of UV radiation alone were tested on a fourth cultivar in a greenhouse compartment with natural background light. Growth chamber plants grown at 60 % or 90 % RH were either exposed to 0.15 W m^{-2} UV radiation for 40 minutes in the middle of the dark period (vegetative plants) or at the end of the light period (EOD, generative plants) or not exposed to UV.

Vegetative 'Christmas Feelings' poinsettia responded strongly to RH. High RH increased plant height, shoot length, the number of leaves per shoot, leaf area, plant diameter and leaf petiole length, while decreasing leaf thickness and internode length. The effects of UV were minor and UV exposure resulted in a decrease in the number of side shoots on the main shoot, a decrease in leaf area and a decrease in petiole length. Generative 'Infinity Red' and 'Bravo Bright Red' poinsettia did not show an obvious stronger morphological response to either RH (60 % and 90 %) or UV alone, and the interaction effects indicate that the RH at which the plants were grown dictates the magnitude and direction of the UV response. Intraspecific differences were found between the two cultivars and the less compact cultivar 'Infinity Red' showed a stronger response to UV compared to the compact cultivar 'Bravo Bright Red'. The stomatal responses of 'Infinity Red' and 'Bravo Bright Red' indicate stronger effects of RH than UV on both leaf and bract conductance measured in both light and dark conditions. Stomatal aperture size of 'Infinity Red' plants was affected by UV in the light, which caused a significant increase in stomatal aperture, while under dark conditions the effect of RH was much stronger and resulted in larger stomatal apertures under 90 % RH than 60 % RH. Photosynthesis in these cultivars showed no effect of RH or UV.

Generative 'Christmas Day' poinsettia grown in a greenhouse compartment at constant RH (70 %) and either exposed to 7.5 minutes of 0.8 W m^{-2} UV EOD radiation or not exposed to UV indicated significant morphological responses to UV radiation, which resulted in a significant decrease in plant height, plant diameter, shoot length, internode length, leaf area and bract area,

and also an increase in both leaf and bract thickness. No significant differences were found in time to flowering. Light response curves of ‘Christmas Day’ poinsettia indicate no effect of UV radiation on photosynthesis, though exposure to UV resulted in higher transpiration and stomatal conductance rates at all light intensities tested.

In summary, the responses to UV radiation in poinsettia were dependent on ontogenetic stage, cultivar, and background climate such as RH and light conditions.

Introduction

Morphological responses to air humidity

High relative air humidity (RH) regimes plague the greenhouse plant production industry, most notably in Northern climates where, in winter, there is a trade-off between ventilating to dissipate humid air and energy saving in closed systems not prone to heat loss (Mortensen 2000). The reported morphological effects of high RH on plants include increased plant height (Grange & Hand 1987; Hoffman et al. 1971; Jeon et al. 2006; Leuschner 2002; Mortensen 1986; Mortensen & Gislerød 1990; Mortensen & Fjeld 1998; Mortensen 2000), increased shoot biomass (Hoffman et al. 1971; Jeon et al. 2006; Mortensen 1986; Mortensen & Gislerød 1990; Mortensen & Gislerød 1999; Mortensen 2000), increased leaf area (Grange & Hand 1987; Hovenden et al. 2012; Jeon et al. 2006; Leuschner 2002; Mortensen 2000), decreased leaf thickness (Leuschner 2002; Torre et al. 2003) and changes in leaf anatomy (Leuschner 2002; Torre et al. 2003) and chlorophyll content (Jeon et al. 2006; Mortensen & Gislerød 1990). The reported results show some variation, for instance, in a study on 23 species of foliage plants Mortensen and Gislerød (1990) found high RH caused an increase in plant height in only five species, while the rest were unaffected. Mortensen (2000) found similar results in that only three of six species tested showed an increase in plant height at high RH, while only two showed an increase in leaf size. Similarly, both Leuschner (2002) and Torre et al. (2003) report finding a decrease in leaf thickness in plants grown at high RH, while Hovenden et al. (2012) reported an increase in leaf thickness at high RH, and Jeon et al. (2006) report an increase in chlorophyll content as a result of growth at high RH, while Mortensen and Gislerød (1990) report a lightening of leaves in several of the species tested in response to high RH. Such differences in findings may be attributed to interspecific differences in response to high RH, though differences in experimental conditions may be the reason authors occasionally report differing responses in the same species (Grange & Hand 1987; Mortensen & Gislerød 1990). Increased leaf area in plants grown at high RH has been associated with photosynthesis and carbon metabolism (Jeon et al. 2006) as photosynthesis has been reported to increase with increases in RH (Grange & Hand 1987). The reduction in leaf thickness reported by Torre et al. (2003) was attributed to a reduction in thickness of the epidermis combined with a reduction in size of both the spongy and palisade mesophyll cells, which further resulted in an increase in the size of the intercellular air-spaces. A similar result was reported by Leuschner (2002), in that plants grown at high RH had less compact mesophyll and larger intercellular air-spaces,

yet the same study also reports an increase in epidermal cell size as a result of growth at high RH. Unfortunately, tall plants with thin leaves are undesirable in commercial plant production, where compact and robust plants are required. Additionally, growth at high RH has a direct negative effect on post-harvest keeping quality of many ornamentals and cut flowers due to high postharvest water loss and lower stress tolerance (Mortensen & Fjeld 1998; Mortensen & Gislerød 1999; Mortensen 2000; Torre & Fjeld 2001; Torre et al. 2003).

Ultraviolet radiation and plants

Ultraviolet (UV) radiation, as UV-A (320-400 nm), UV-B (280-320 nm) and UV-C (<280 nm), has pleiotropic effects on plant growth and development, including a reduction in elongation growth, thickening of leaves, thickening of cuticular wax, production of phenolic screening compounds and reduction in photosynthetic capacity (Frohnmeyer & Staiger 2003; Mackerness et al. 1998; Strid et al. 1994; Wargent et al. 2009). The two means of coping with exposure to UV radiation comprise of tolerance and avoidance, where tolerance involves the induction of intrinsic repair mechanisms, while avoidance relates primarily to the production of secondary screening compounds for protection (Frohnmeyer & Staiger 2003; Jenkins 2014). Many studies have focused on the detrimental effects of UV radiation on plants (e.g. Strid et al., 1994, Mackerness et al., 1998), as damage to the ozone layer my increase UV radiation to harmful levels in the future (Strid et al. 1994). Damaging UV-B radiation targets plants in several areas, including the thylakoid membrane of the chloroplast and, at the molecular level, mRNA transcription and protein synthesis (Strid et al. 1994). Photomorphogenic responses to UV radiation are mediated by the recently discovered photoreceptor UV RESISTANCE LOCUS8 (UVR8) (Rizzini et al. 2011), which regulates the expression of numerous genes underlying these responses (Jenkins 2014). UVR8 signalling involves genes encoding the ELONGATED HYPOCOTYL5 (HY5) transcription factor, which in turn mediates responses of the UVR8 dependent pathway (Brown & Jenkins 2008; Cloix et al. 2012; Tossi et al. 2014), the closely related HY5 HOMOLOG (HYH) transcription factor (Brown & Jenkins 2008; Tossi et al. 2014), and CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1) (Tossi et al. 2014), which functions together with UVR8 to control photomorphogenic responses to UV radiation (Cloix et al. 2012). Such photomorphogenic responses which occur at low doses of UV radiation are often not associated with damage (Cloix et al. 2012; Jenkins 2014), and include inhibition of hypocotyl extension, induction of cotyledon opening (Jenkins, 2014 and references therein), and the most well-known response, the biosynthesis of flavonoids. UVR8

regulates the transcription of a set of approximately 70 genes in mature *Arabidopsis* plants, many of which are associated with prevention against, and repair of, UV-B radiation damage (Cloix et al. 2012; Jenkins 2014), though other associations include encoding for chloroplast proteins and other metabolic activities. This regulation occurs over a wide range of UV fluence rates, and the exact number of signalling pathways is as yet still unknown (Jenkins 2014).

Morphological responses to UV radiation

Plant morphological responses to UV radiation have been thoroughly investigated over the past several decades for a large range of species under field conditions (Baroniya et al. 2011; Gehrke et al. 1996; Grammatikopoulos et al. 1998; Johanson et al. 1995; Lingakumar et al. 1999; Nedunchezhian & Kulandaivelu 1997; Rozema et al. 2006; Singh et al. 2012), greenhouse conditions (Deckmyn & Impens 1998; Deckmyn & Impens 1999; Meijkamp et al. 2001; Nogués et al. 1998) and in controlled environment growth chambers (Barsig & Malz 2000; Cen & Bornman 1990; Kakani et al. 2003; Koti et al. 2007; Liu et al. 1995; Mackerness et al. 1998; Nogués et al. 1998; Qaderi et al. 2008; Surabhi et al. 2009), and have been the subject of several reviews (Caldwell et al. 1995; Frohnmeyer & Staiger 2003; Hollosy 2002; Jansen et al. 1998; Jenkins 2009; Mpoloka 2008; Teramura & Sullivan 1994; Tossi et al. 2009). Results of morphological findings across field, greenhouse and controlled environment chambers show general agreement, with the most commonly found responses to elevated UV levels being a reduction in plant height (Deckmyn & Impens 1998; Deckmyn & Impens 1999; Gehrke et al. 1996; Johanson et al. 1995; Kakani et al. 2003; Koti et al. 2007; Meijkamp et al. 2001; Qaderi et al. 2008; Singh et al. 2012), increased leaf thickness (Bornman & Vogelmann 1991; Cen & Bornman 1990; Frohnmeyer & Staiger 2003; Gehrke et al. 1996; Grammatikopoulos et al. 1998; Johanson et al. 1995; Liu et al. 1995; Meijkamp et al. 2001; Teramura & Sullivan 1994) and reduced leaf area (Cen & Bornman 1990; Frohnmeyer & Staiger 2003; Kakani et al. 2003; Koti et al. 2007; Meijkamp et al. 2001; Nogués et al. 1998; Qaderi et al. 2008; Wargent et al. 2009), with UV-B exclusion experiments showing converse agreement, in that UV-B exclusion enhanced plant height and leaf area (Baroniya et al. 2011; Lingakumar et al. 1999). However, there have also been many exceptions to the general findings. For instance, Grammatikopoulos et al. (1998) found neither plant height nor leaf area of *Laurus nobilis* and *Ceratonia siliqua* to be affected by increased UV radiation, and Rozema et al. (2006) found similar UV resistance in leaf area and leaf thickness of tundra plants in the high Arctic. Liu et al. (1995) found no effects of enhanced UV on leaf area in *Hordeum vulgare* (barley), and while there was a

reduction in the rate of growth there was no effect on total plant height. Gehrke et al. (1996) and Johanson et al. (1995) found leaf thickness to increase in an evergreen species (*Vaccinium vitis-idaea*) in response to enhanced UV radiation, yet in two deciduous species (*Vaccinium myrtillus* and *Vaccinium uliginosum*) the leaves were thinned, as were the leaves of *Gossypium hirsutum* (cotton) found by Kakani et al. (2003). Nedunchezhian and Kulandaivelu (1997) found results that oppose the general findings, in that exposure to enhanced UV radiation caused an increase in both plant height and leaf area in *Vigna unguiculata*. Further morphological responses to enhanced UV radiation include reduced plant and leaf biomass (Baroniya et al. 2011; Cen & Bornman 1990; Deckmyn & Impens 1999; Koti et al. 2007; Nogués et al. 1998; Surabhi et al. 2009; Teramura et al. 1991), reduced chlorophyll content (Cen & Bornman 1990; Koti et al. 2007; Lingakumar et al. 1999; Nedunchezhian & Kulandaivelu 1997; Qaderi et al. 2008), changes in epicuticular wax content (Barsig & Malz 2000; Kakani et al. 2003; Koti et al. 2007; Qaderi et al. 2008) and leaf bronzing (Jansen & van den Noort 2000; Mackerness et al. 1998), though variations in plant responses have been reported for these parameters as well. Such variation in reported results highlights the plasticity in plant responses to UV radiation, which clearly depend on both internal factors within the plant (genetics, ontogenetic stage, acclimatisation, species) and external environmental factors (light intensity, light quality, photoperiod, temperature, CO_2 concentration) to drive both the response magnitude and direction. Additionally, several studies have shown a correlation between the amount of background PAR given in addition to UV exposure and the resistance of plants to UV-induced damage, with high background PAR providing protection from harmful UV effects (Jansen et al. 1996; Teramura & Sullivan 1994). Cen and Bornman (1990) found that *Phaseolus vulgaris* showed decreased leaf area, decreased leaf dry weight, decreased leaf chlorophyll content, inhibition of photosystem II and generally greater sensitivity to UV damage in plants exposed to UV and low level PAR in comparison to those plants exposed to UV and high level PAR and control plants. Jansen et al. (1996) show the degradation of both D1 and D2 proteins of photosystem II to be dependent on the fluence rate of background PAR. This dependence on background PAR for resistance to UV-induced damage lies in the dependence on PAR to drive morphological and physiological processes, which in turn provide resistance (Jansen et al. 1996).

Stomatal responses to RH

The effects of high relative air humidity (RH) during growth may be detrimental to greenhouse production species, as growth at high RH results in the production of malfunctioning stomata (Fanourakis et al. 2011; Torre & Fjeld 2001) through effects on abscisic acid (ABA) regulation (Arve et al., 2013). Several studies on roses have demonstrated the detrimental effect of high air humidity, the threshold being > 85 %, on the functioning of stomata (Arve et al. 2013; Torre & Fjeld 2001; Torre et al. 2003), thereby affecting their post-harvest keeping quality (Mortensen & Gislerød 1999). After growth at high RH, *Corylus maxima* cuttings and intact plants both show malfunctioning stomata, with > 50 % of expanding leaves showing an expansion inhibition due to the inability of stomata to close (Fordham et al. 2001). The same effect, though to a slightly lesser extent, was found in young, fully expanded leaves of *Tradescantia virginiana* (Rezaei Nejad & Van Meeteren 2005), which, like roses (Torre et al. 2003) and micropropagated *Delphinium* plants (Santamaria et al. 1993), show significantly larger stomata in plants grown at high (90 ± 5 %) compared to moderate (55 ± 5 %) RH. Interactions between response pathways to differing environmental signals is highly dependent on species specific traits and environmental conditions (Aasamaa & Sober 2011), with one signal often dominating over the other(s). In tree species responses to changes in RH have been found to dominate over responses to changes in photosynthetic factors (ambient CO_2 concentration and light intensity) when given simultaneously (Aasamaa & Sober 2011). Malfunctioning stomata in plants grown at high RH show failure to respond to stomatal-closing signals, such as darkness (Fordham et al. 2001) and ABA application (Santamaria et al. 1993). Stomatal control is regulated by the phytohormone ABA, levels of which increase during the dark period in order to induce stomatal closure (Arve et al. 2013). Plants grown under constant high RH show lower levels of ABA in general (Arve et al. 2013; Rezaei Nejad & van Meeteren 2008), a result which is more likely due to ABA inactivation than an effect on ABA biosynthesis (Arve et al. 2013). High RH plants also show a failure to increase ABA levels during the dark period, which results in a lack of signal for stomatal closure, causing dark transpiration (Arve et al. 2013). Excessive transpiration during growth and the inability to respond to stomatal cues leaves plants vulnerable to excessive water loss upon removal to a drier environment. Excessive transpiration may also result in further detrimental effects to the plants, such as calcium (Ca) deficiency (Francois et al. 1991; Gislerød 1999) leading to bract necrosis in Poinsettia (Gislerød 1999), a fact that emphasises the need for investigation into ways of preventing malfunctioning stomata in high RH environments.

Stomatal responses to UV radiation

UVR8 was found to regulate stomatal density in the presence of UV-B radiation in *Arabidopsis* (Wargent et al. 2009), but the exact role of UV-B in stomatal density control is not yet fully elucidated (Jenkins 2014). According to Tossi et al. (2014), UVR8-regulated responses in stomatal movement are mediated by nitric oxide (NO), a biologically active molecule in several plant processes. The authors demonstrate how both NO and hydrogen peroxide (H_2O_2) increase in concentration in response to increasing UV fluence rates, with NO facilitating stomatal closure for up to 24 h after the beginning of exposure. Tossi et al. (2009) reported previously an increase in ABA concentration in maize (*Zea mays*) plants irradiated with UV and subsequently demonstrate that ABA is required for NO-induced protection against UV-induced deleterious effects. Tossi et al. (2014) propose a model for UVR8 signalling in guard cells (see Figure 1), in which UVR8 interaction with COP1 stimulates the expression of HY5 and HYH, at the same time as UV-B induces an increase in ABA concentration, in turn activating H_2O_2 and NO production via NADPH oxidase (pNOX) and nitrate reductase (NR). NO then deactivates inward K^+ channels and activates outward ion channels, which brings about a loss of turgor pressure and thereby stomatal closure (Tossi et al. 2014). In this way stomatal closure may be regulated by UV radiation, providing a potential means of combatting high rates of water loss from malfunctioning stomata.

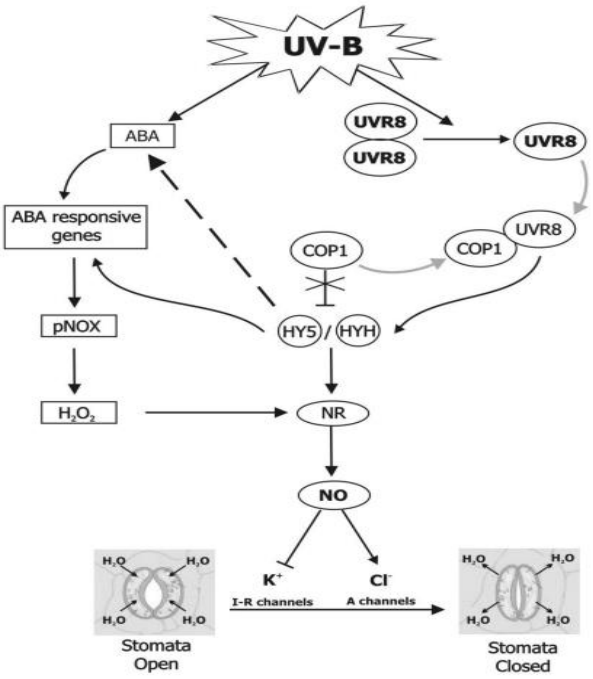


Figure 1. Illustration of the proposed UVR8 signalling pathway in guard cells. See text for full explanation. Black arrows indicate induction, black bars indicate inhibition, grey arrows indicate protein interactions. Dashed line indicates a hypothetical cell response. Adapted from Tossi et al. (2014).

Photosynthetic and phenolic responses to RH and UV

The response of photosynthesis to an increase in RH has been little studied, though an increase in photosynthetic carbon assimilation has been reported in plants exposed to high RH (Grange & Hand 1987). This increase is most likely the result of an indirect effect of high RH which results in the opening of stomata, allowing for a higher rate of CO_2 assimilation for photosynthesis. UV radiation, on the other hand, has been shown to have both direct and indirect effects on plant photosynthesis. Photosystem II has been shown to be the main target for direct UV-induced damage to photosynthesis (Hollosy 2002; Strid et al. 1994), where UV exposure reduces the oxidative capacity, causes photoreduction of plastoquinones and results in enhanced degradation and turnover of both the D1 and D2 polypeptides (Jansen et al. 1996; Teramura & Sullivan 1994). Additionally, UV radiation reduces the integrity of the thylakoid membrane, reduces the activity of Rubisco and decreases the levels of photosynthetic pigments (Frohnmeyer & Staiger 2003; Hollosy 2002; Jansen et al. 1998), though such findings are often observed under particularly high UV fluence rates (Jansen et al. 1998). Indirect effects on plant photosynthetic capacity by exposure to UV radiation may result from UV-induced changes in stomatal function, alterations to leaf anatomy and increasing of leaf thickness resulting in diminished penetration of photosynthetically active radiation (PAR) to photosynthetic centres, and UV-induced morphogenic responses which may result in canopy alteration (Hollosy 2002). The accumulation of flavonoids in response to UV radiation is well-documented (Guo et al. 2008; Hollosy 2002; Mahdavian et al. 2008; Mpoloka 2008), and these secondary metabolites assist in reducing damage by UV radiation to the plant by attenuating the amount that reaches the photosynthetic apparatus (Mahdavian et al. 2008; Stapleton & Walbot 1994). Anthocyanins are a class of flavonoids and are derived from anthocyanidins in the phenylpropanoid pathway (Guo et al. 2008). They form the largest group of water-soluble pigments in the plant kingdom and are visible in the red, purple and blue colours seen in flowers, fruits and berries (Guo et al. 2008). Little information is available on the effects of RH on anthocyanin content in plants, yet UV radiation has been shown to induce upregulation of anthocyanin biosynthetic genes (Guo et al. 2008; Martinez-Luscher et al. 2014).

Poinsettia

Poinsettia is one of the most economically important potted plant species in Norway, with an annual production of approximately six million plants (Strømme 1994). As Norway lies between 58 and 72 °N, autumn and winter bring a severe decline in day length and natural

irradiance. As a result of this most production plants for which production time coincides with autumn and winter, such as poinsettia, need to be cultivated under supplemental lighting regimes in greenhouses (Bævre et al. 1994). Poinsettia are short day (SD) plants with a critical day length of approximately 12.5 hours, but in commercial production 10 hours light is commonly used for fast floral induction and differentiation. Excessive stem elongation has been a problem in poinsettia production for many years, and chemical growth regulators have been used as a means of regulation (Berghage & Heins 1991). However, restrictions on the use of chemical growth regulators have been becoming more prominent since the beginning of the century (Mortensen 2000) and means of controlling plant height and other desirable morphological traits without the use of chemicals still needs further investigation. There have been several studies correlating the effects of the difference between day and night temperature (DT and NT respectively) to poinsettia stem elongation (Berghage & Heins 1991; Moe et al. 1992a), and Mortensen (2000) showed how increased RH resulted in increased plant height, increased diameter, increased leaf size and increased dry weight of the plants, not all of which are desirable traits in commercial production. As high RH seems to be unavoidable in greenhouses in winter without excessive energy consumption due to a trade-off between ventilating and heating, methods of offsetting undesirable consequences of high RH using non-chemical means need further investigation. Poinsettia will be used as a model plant in this experiment as they have been shown to be susceptible to the development of adverse morphological traits when grown at high RH, and indicate easily undesirable effects such as excessive elongation and calcium (Ca) deficiency (bract necrosis). Furthermore, with poinsettia being such an economically important species it is paramount to determine the means to produce the highest quality plants by the best, lowest energy and chemical consumption means possible.

Plant responses to UV radiation are pleiotropic and are seen in many aspects of plant development, morphology and physiology. Many responses are consequential of a host of factors, including UV radiation dose and light wavelength (both UV and background PAR), as well as environmental factors such as CO_2 concentration, water stress and temperature. Plant responses to high RH are more uniform and are seen in aspects of plant growth, though are most prominent and most thoroughly investigated in plant stomatal function and water relations. Here we present the responses of four poinsettia cultivars to either UV radiation as the sole changing environmental factor during growth in a greenhouse, or to UV radiation given

in combination with one of two levels of RH in both vegetative and generative stages of growth in controlled environment chambers. The plants and experimental conditions were not chosen to mimic those of field conditions, nor the UV radiation dose or spectrum used chosen to mimic that of solar radiation. Rather, the study was undertaken in order to investigate the responses of a highly commercial production species, *Euphorbia pulcherrima* (Willd ex. Klotzsch), to UV radiation for the purpose of finding ways to potentially improve production methods though counteracting the adverse effects of high RH, a condition frequently found in commercial greenhouse production during winter at higher latitudes. The use of chemical growth regulators is becoming more and more restricted, and therefore alternative means for control of plant growth and morphology need to be assessed. The regulation of stomata by UV radiation may provide a means of offsetting the malfunctioning stomata caused by growth in a high RH environment. Furthermore, the use of UV radiation as a means of controlling plant height will be explored, in the hope of potentially using this as a means of decreasing the use of chemical growth regulators. Additionally, since many of the greenhouses have cladding material that does not transmit UV radiation, the use of artificial UV could be an alternative in commercial production to expose plants to UV. Several reports have also shown that UV lamps can be used to control diseases such as powdery mildew (Suthaparan et al. 2012; Suthaparan et al. 2014) and botrytis (Demkura & Ballare 2012). Botrytis (greymold) is one of the main problems during and after production of poinsettia and tools that could help to control morphology and diseases would be of great interest in commercial greenhouse production.

The use of cellulose acetate (CA) filters in investigations with UV radiation is widely used as a means of preventing UV-C (and some UV-B) radiation from reaching the plants, through filtering out wavelengths below 290 nm (Middleton & Teramura 1993). Studies wishing to investigate the effects of UV-B radiation often use a combination of CA and Mylar filters, which remove UV-B radiation and allow only UV-A radiation to reach the plant (Sampath-Wiley & Jahnke 2011; White & Jahnke 2004). This ideology is essentially flawed as plant responses are shaped by the ratio of fluences (Teramura & Sullivan 1994), meaning the combination of UV-A and UV-B will induce responses different to those of UV-B alone (e.g. photoreactivation). Unscreened fluorescent lamps were chosen for this investigation as the study was not geared to specific wavelength (e.g. UV-B), and was rather to investigate the practical potential of such a light source in ameliorating the detrimental effects of high RH.

Materials and Methods

Experiment 1: Vegetative growth of poinsettia

Pre-Cultivation

Cuttings of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) of the cultivar 'Christmas Feelings', rooted in Jiffy-7 (Jiffy International AS, Kristiansand, Norway) were obtained from Ljones Gartneri AS in December 2013 and potted in 12 cm pots with Sphagnum peat growth medium, 6 % ash, pH 5.0 -6.0 (Degernes Torvstrøfabrikk AS, Degernes, Norway). The rooted cuttings were placed in a greenhouse compartment at 21 °C, 70 % RH and ambient CO_2, controlled using a PRIVA system (Priva, De Lier, The Netherlands), and receiving 100 µmol m^{-2} s^{-1} PAR from high pressure sodium (HPS) lamps (Osram NAV T-400W, Munich, Germany) for an initial growth period. PAR intensity was measured using a Li-Cor Model L1-250 Quantum sensor (Li-Cor Inc., Lincoln, NE, USA). The plants were pinched over 3-4 leaves and two weeks later the new shoots were approximately three centimetres. The plants were then moved to controlled environment growth chambers for UV exposure.

Experimental set-up

The plants were subjected to long day (LD) treatment, with a 20/4 hour light/dark photoperiod regime receiving PAR radiation at 150 µmol m^{-2} s^{-1} from HPS lamps (Table 1). Four treatments were used (n = 5 for each treatment) over a period of eight weeks, and plants were either exposed to (+UV) or not exposed to (-UV) UV radiation in addition to the light from the HPS lamps, at either moderate (60 %) or high (90 %) RH, indicated as 60+UV, 60-UV, 90+UV and 90-UV respectively. UV radiation was supplied for 40 minutes in the middle of the dark period at a fluence rate of 0.15 W m^{-2} (Figure 3). UV radiation was provided by unscreened fluorescent tubes (Q-panel UV 313, Q-Lab Corporation, Ohio, USA), and measured using a Skye SKU 430/SS2 UVB Sensor connected to a Skye SpectroSense2 Meter (Skye Instruments Ltd, Llandrindod Wells, Powys, UK). Temperature was maintained at 21°C in all chambers by a PRIVA system. Prior to placement in the growth chambers excessive shoots were removed from each plant, leaving four shoots. Plants were sprayed with Bayer Confidor (0.35 g l^{-1}, Yates, of DuluxGroup Limited, Victoria, Australia) twice over the course of the experiment. The plants were watered three times a week with 50/50 mixture of YaraLiva® Calcinit™ calcium nitrate solution (14.4 % NO_3, 1.1 % NH_4, 19.0 % Ca, Yara Norge AS, Oslo, Norway)

and Kristalon™ Indigo (7.5 % NO_3, 1 % NH_4, 4.9 % P, 24.7 % K, 4.2 % Mg, 5.7 % S, 0.027 % B, 0.004 % Cu, 0.06 % Mn, 0.2 % Fe, 0.004 % Mo, 0.027 % Zn, Yara Norge AS, Oslo, Norway) and four times a week with plain water. Nemasys® *Steinernema feltiae* nematodes (formerly Becker Underwood, West Sussex, UK, now BASF Crop Protection, Limburgerhof, Germany) were used to combat fungus gnats.

The UV sensor was calibrated to sunlight and readings were compared to solar spectral measurements taken using an Optronic OL756 Spectroradiometer (Optronic Laboratories, Inc., Florida, USA), revealing the need to multiply the readings taken using the Skye UV sensor by 0.84 in order to get absolute UV readings, or by 0.88 to obtain the biological effect of unscreened UV tubes. Figure 2 shows the spectral power distribution for the lamps used in the experiments. The lamps produce ultraviolet light mostly in the UV-A (320-400 nm) and UV-B (280-320nm) regions, though there is a small amount of UV-C (< 280 nm) produced in addition.

Table 1. Controlled environment growth chamber conditions for each of the experiments performed.

	Temperature (°C)	RH (%)	PAR Irradiance (μmol m^{-2} s^{-1})	UV Radiation (W m^{-2})	UV Dose Duration, time of day	Absolute UV Dose (W m^{-2} day^{-1})	Day/Night Length (h)	Daily Light Integral (mol m^{-2} d^{-1})
Experiment 1	21	60 or 90	150	0.15	40 mins, night	360	20/4	10 800
Experiment 2	22	60 or 90	150	0.15	40 mins, EOD	360	10/14	5 400
Experiment 3*	20	70	150	0.80	7.5 mins, EOD	360	10/14	5 406

* Natural light in the experimental period: 6 mol m^{-2} d^{-2} average across 84 days of the experiment.

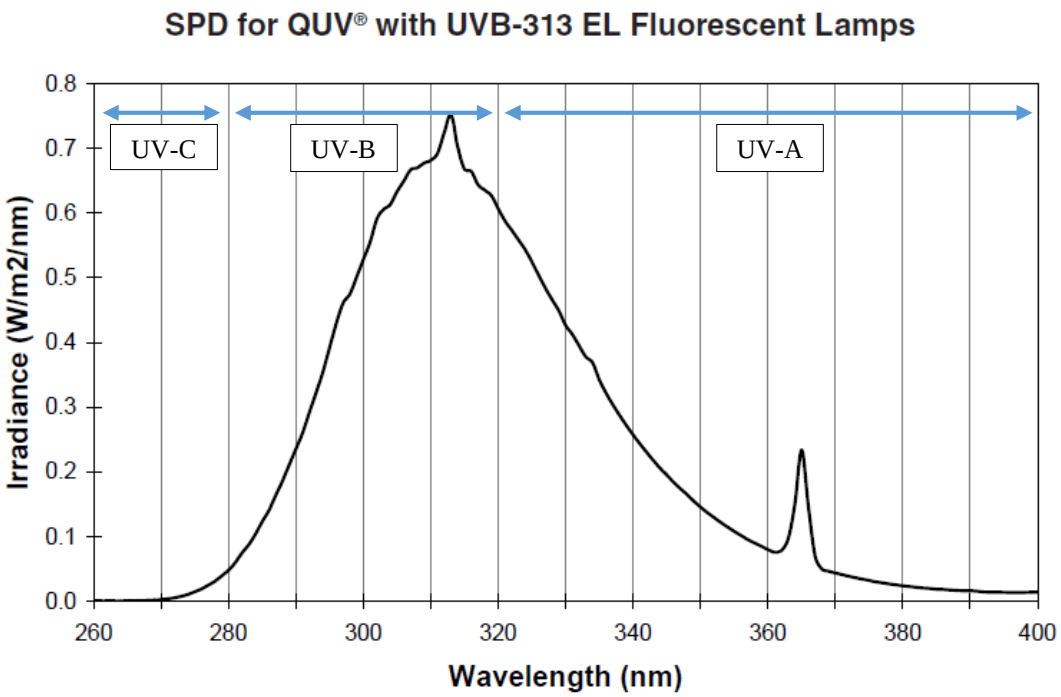


Figure 2. Spectral power distribution (SPD) for Q-panel UV 313 lamps (Q-Lab Corporation, Ohio, USA) measured in W m^{-2} nm^{-1}. Adapted from Q-Lab Corporation (2011). UV-A, UV-B and UV-C regions are indicated.

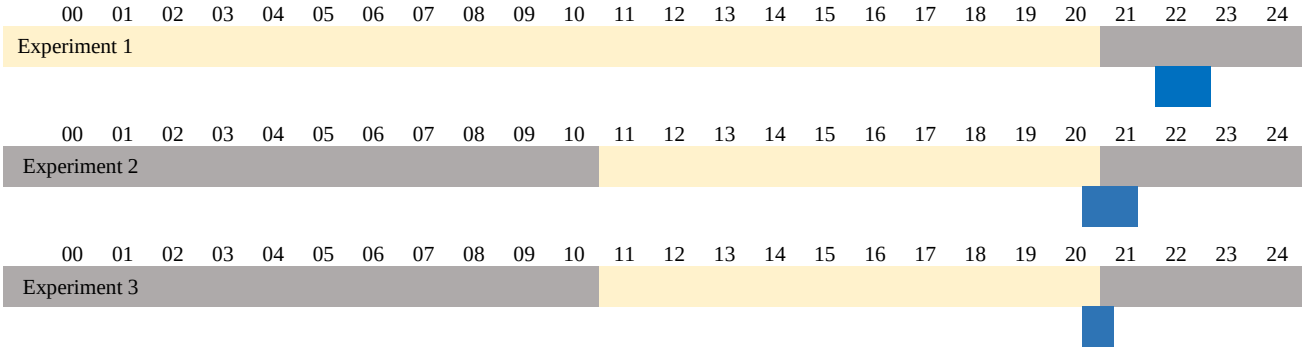


Figure 3. Light and dark periods (numbers indicate time) of Experiments 1, 2 and 3, indicating time and approximate duration of UV radiation (not to scale, for exact length of UV radiation see Table 1). UV radiation overlapped with the light period for five minutes in both Experiments 2 and 3, while UV radiation was given in the middle of the dark period in Experiment 1.

Growth data sampled at the end of the experiment

56 days after the start of LD treatment the plants were harvested for growth and water loss analyses. Plant height from the rim of the pot to the shoot apical meristem, plant diameter, shoot length, petiole length (as average of the three longest petioles on the two longest shoots) and leaf area were measured, leaf area was measured using a LI-3100 Area Meter (Li-Cor, Inc., Lincoln, Nebraska, USA); the total number of leaves was counted, from which the average number of leaves per shoot could be calculated; the number of side shoots on the longest shoot were counted and the fresh weights (FW) and dry weights (DW) of leaves and the stem of the longest shoot were measured, from which the specific leaf area (SLA) was calculated using the following equation:

Eq. i) $SLA = \frac{\text{Leaf Area } (cm^2)}{\text{Leaf DW } (g)}$ †

†note: for SBA Bract Area (cm^2) is used

Average internode length was calculated by dividing the number of leaves per shoot by the average shoot length. A separate water loss test was performed on four detached leaves from each treatment. The leaves were weighed directly after detachment from the plant, as well as three hours after the initial weighing to determine water loss by weight (%) over the course of the three hour period. Plant photographs were taken 56 days ASD using a Samsung Galaxy S3 GT-19305 (Samsung Electronics Co., Ltd., Suwon, South Korea).

Experiment 2: Generative growth of poinsettia

Pre-cultivation

Cuttings of two poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) cultivars, 'Infinity Red' and 'Bravo Bright Red' (n = 40 for each cultivar), were obtained in June 2014 from GASA Young Plants (GASA GROUP Denmark A/S, Odense, Denmark). The rooted cuttings were pinched above four leaves and potted in 12 cm pots with Sphagnum peat growth medium, 6 % ash, pH 5.0 -6.0 (Degernes Torvstrøfabrikk AS, Degernes, Norway). The plants were then transferred to controlled growth chambers and exposed to long day (LD) treatment (20/4 hour light/dark photoperiod regime), 22 °C, ambient CO_2 and 70 % RH for 16 days prior to the short day (SD) treatments. Light was supplied at 150 µmol m^{-2} s^{-1} by HPS lamps (see Experiment 1).

Experimental set-up

The plants were exposed to SD treatment with 10/14 hour light/dark photoperiod regime, as well as four growth treatments (same as Experiment 1: 60-UV, 60+UV, 90-UV and 90+UV) in which plants were exposed to either moderate (60 %) or high (90 %) RH and either no UV radiation (-UV) or 40 minutes of 0.15 W m^{-2} UV radiation (+UV) at the end of the light period (EOD). EOD UV radiation overlapped with the light period for five minutes (Figure 3). Temperature was maintained at 22 °C and the CO_2 levels at 400 ppm (Table 1) by a PRIVA system. The plants were rotated in the chambers for even light distribution and were sprayed with Bayer Confidor (0.35 g l^{-1}, Yates, of DuluxGroup Limited, Victoria, Australia) three times over the course of the experiment. Note on SD treatment: due to a misunderstanding the two –UV chambers received LD treatment between 04 and 06 July 2014 (11-13 days ASD) and due to a faulty compressor the two 90 % RH chambers received 70 % RH from 16-17 July 2014 (23-24 days ASD). The plants were watered according to the same regime described for Experiment 1. Time to flowering (visible cyathia) was recorded.

Plant growth measurements during and at the end of the experiment

The plants were pinched and three main shoots were allowed to develop per plant. Plant height from the rim of the pot to the shoot apical meristem, plant diameter and shoot length of all three shoots were measured and the total number of side shoots were counted 16 days ASD. The measurements were repeated 28 days ASD. Final plant harvest and chlorophyll content measurements, using a CL-01 Chlorophyll Content Meter* (Hansatech Instruments Ltd., Norfolk, UK), were conducted 58 days ASD, during which plant height from the rim of the pot to the shoot apical meristem and plant diameter were measured for each plant, while shoot length, petiole length of the three longest leaves and bracts, leaf area, bract area (using a LI-3100 Area Meter (Li-Cor, Inc., Lincoln, Nebraska, USA)), FW of shoots, leaves and bracts and DW of shoots, leaves and bracts were all measured for each shoot, and the number of leaves, bracts and side shoots were counted for each shoot. SLA, specific bract area (SBA) (Eq. i) and average internode length (mean leaves per shoot/mean shoot length) were calculated, as well as the percentage of biomass found in shoots, leaves and bracts (shoot, leaf or bract DW/total DW^x100). * Chlorophyll Content Meter measurements are relative, therefore no unit is given for chlorophyll content in results. Plant photographs were taken 28 and 58 days ASD using a Samsung Galaxy S3 GT-19305 (Samsung Electronics Co., Ltd., Suwon, South Korea).

Photosynthesis and conductance measurements

Measurements of plant photosynthesis and transpiration rates were taken in the growth chambers 28 and 38 days ASD, using a 2.5 cm^2 cuvette (PLC Standard, PP Systems, Norfolk, UK) attached to a CIRAS-1 portable photosynthesis system (PP Systems, Norfolk, UK). CO_2 concentration in the cuvette was maintained at ambient levels (400 ppm) and cuvette temperature at 21°C. Light settings were set at 'Tungsten' and recording was done manually. Additional conductance measurements were taken using an AP4 Porometer (Delta-T Devices Ltd., Cambridge, UK) 44 days ASD as initial conductance measurements were corrupted in the high RH treatments. These measurements were taken outside the chambers where the RH was approximately 45-50 %.

Stomata measurements: imprints and microscopy analyses

Leaf impressions (approx. 0.5 cm^2) were taken using Suzuki's Universal Micro-Printing Method (SUMP Laboratory, Tokyo, Japan) as previously described (Tanaka et al. 2005) for observation of stomata on leaves (n = 3 imprints for each treatment under light and dark conditions). Leaf impressions were analysed using a Leica DM 5000 B light microscope connected to a CTR 5000 electronics box. This was attached to a Leica DFC 425 digital microscope camera with a Leica 10445929 0.5x video objective (all Leica Microsystems GmbH., Wetzlar, Germany). Pictures and digital analysis were carried out using Leica Application Suite v4.3.0 (Leica Microsystems GmbH, Wetzlar, Germany) in order to obtain pictures (n = 5 for each impression, therefore n = 15 for each treatment) and determine average stomatal aperture size.

For scanning electron microscopy (SEM) samples were taken from both leaves and bracts and preserved in fixatives containing PIPES buffer, (pH 7), 1.2 % glutaraldehyde (GA) and 2 % paraformaldehyde (PF). The samples were dehydrated through an ethanol series before being subjected to critical point drying using a Bal-Tec CPD 030 Critical Point Dryer (Formerly Bal-Tec AG, Liechtenstein, now Leica Microsystems GmbH, Wetzlar, Germany). Samples were then mounted for analysis and coated with gold-palladium using a Polaron SC7640 Sputter Coater (Quorum Technologies Ltd., East Sussex, UK). SEM analyses of stomata were then carried out using a Zeiss EVO 50 Scanning Electron Microscope (Carl Zeiss Microscopy GmbH, Jena, Germany). Pictures of each stomate (n = 3 for each leaf sample, n = 1 for each

bract sample) were taken at 20 000/15 000 and 3 000 x magnification (20 KeV, Iprobe at 30). An overview picture (500 x magnification) was taken for each sample.

Experiment 3: Generative growth of poinsettia in a greenhouse

Pre-cultivation

Cuttings of the Poinsettia cultivar "Christmas Day" (*n* = 35), rooted in Jiffy-7 (Jiffy International AS, Kristiansand, Norway) were obtained from Ljones Gartneri AS in September 2014. The cuttings were potted in 12 cm pots with Sphagnum peat growth medium, 6 % ash, pH 5.0 -6.0 (Degernes Torvstrøfabrikk AS, Degernes, Norway) and sprayed with Bayer Confidor (0.35 g l^{-1}, Yates, of DuluxGroup Limited, Victoria, Australia), before being watered again with Confidor seven days after potting and pinched above four leaves the following day. The plants were then placed in a greenhouse chamber at 21 °C, 70 % RH and ambient CO_2, controlled by a PRIVA system, receiving 100 µmol m^{-2} s^{-1} of PAR provided by HPS lamps (see Experiment 1) for 20 days for initial plant development.

Experimental set-up

The plants were moved to a separate greenhouse chamber and subjected to SD treatment (10/14 hour light/dark photoperiod regime) with natural daylight and additional artificial irradiance of 150 µmol m^{-2} s^{-1} provided by HPS lamps. Two growth treatments were used in which plants received either no UV radiation (-UV) or seven minutes of 0.8 W m^{-2} EOD UV radiation (+UV), overlapping the light period by five minutes (see Figure 3). Temperature was maintained at 20°C, RH at 70 % and CO_2 at ambient levels (400 ppm) using a PRIVA system. The +UV plants were rotated daily under the UV lamps for even light distribution. The plants were watered according to the same regime described for Experiment 1.

Plant growth measurements during and at the end of the experiment

Measurements of plant height from the rim of the pot to the shoot apical meristem, plant diameter and shoot length were taken 16 and 28 days ASD for growth curve analysis and plants were pinched and three main shoots were allowed to develop per plant from 28 days ASD. Final harvest (*n* = 10 for each treatment) was done 63 days ASD, during which plant height from the rim of the pot to the apical meristem, plant diameter, leaf area and bract area were

measured for each plant, and shoot length, average leaf petiole length of the first three petioles per shoot and fresh and dry weights of leaves, bracts and stems were measured for each shoot, while the total number of leaves and bracts were counted. SLA and SBA were calculated (Eq. i) from leaf and bract area. The average internode length was calculated by dividing the average number of leaves per shoot by the average shoot length. This experiment was performed in the hope of mimicking actual growth of commercial poinsettia in all aspects with the exception of the use of growth retardant chemicals, which were replaced, in this case, with the addition of UV radiation. The control group received neither growth retardant chemicals nor UV radiation (-UV group). Time to flowering (visible cyathia) was recorded.

Light response curve measurements

Measurements of photosynthesis and transpiration were taken for light-response curve analysis at 44 and 46 days ASD, using a 2.5 cm^2 cuvette (PLC Standard, PP Systems, Norfolk, UK) attached to a CIRAS-1 portable photosynthesis system (PP Systems, Norfolk, UK). This was performed by measuring leaf photosynthesis, transpiration and conductance at an initial irradiance of 550-600 µmol m^{-2} s^{-1} and from there decreasing it to ~50 % of that (300-350 µmol m^{-2} s^{-1}), ~25 % (160-180 µmol m^{-2} s^{-1}), ~10 % (60-90 µmol m^{-2} s^{-1}), ~5 % (40-50 µmol m^{-2} s^{-1}), ~2.5 % (20-25 µmol m^{-2} s^{-1}) and 0 % (0 µmol m^{-2} s^{-1}) using grey filters and finally aluminium foil, measuring the same parameters at each irradiance (n = 5 for each treatment for each irradiance, two replicate measurements taken from each plant). Further conductance measurements were taken 36 days ASD using an AP4 Porometer (Delta-T Devices Ltd., Cambridge, UK) for comparisons between light and dark conductance (n = 10 for each treatment for each light condition, two replicate measurements taken from each plant). CO_2 concentration in the cuvette was maintained at ambient levels (400 ppm) and cuvette temperature at 21°C. Light settings were set at 'Tungsten' and recording was done manually.

Anthocyanin content analyses

Samples from bracts were taken for anthocyanin content analysis. Discs of 0.45 cm^2 were removed from the reddest bracts (n = 5) using a cork borer and stored in Eppendorf tubes with methanol (CH_4O) and 1 % hydrochloric acid (HCl). These were left overnight at 4°C before being analysed for anthocyanin content using a UV-1800 UV-VIS Spectrophotometer (Shimadzu, Kyoto, Japan) with an absorbance peak at 530 nm.

Statistical Analyses

All statistical analyses were performed using RStudio version 0.98.1062 (© 2009-2013 RStudio, Inc.). All data were tested for normality using both Normal Quantile plots and Shapiro-Wilk Normality tests, as well as tested for homoscedasticity using Levene's Test for equality of variances. Testing of differences between treatments was performed using two-way ANOVAs where the data displayed normality. In cases of non-normality the data were analysed for main effects using Kruskal-Wallis Rank Sum tests, while interaction effects for non-normal variables were obtained using the Adjusted Rank Transform test (Leys & Schumann 2010). In cases if heteroscedasticity data from Experiment 3 were analysed using a One-Way Analysis of Means not assuming equal variance as UV radiation was the only factor. In Experiments 1 and 2 main effects for heteroscedastic variables were obtained using One-Way Analyses of Means for each factor, while interaction effects were determined using a One-Way Analysis of Means on Adjusted Rank Transformed data.

Results

Experiment 1: Vegetative growth of poinsettia

Morphological parameters

Growth and morphology of 'Christmas Feelings' Poinsettia grown in long day conditions was significantly affected by RH, but only minor effects of UV radiation were found (Table 2). Plant height and plant diameter were 17 % and 13 % larger in plants grown in high RH compared to moderate RH respectively. Similarly, increases in shoot length (36 %), number of leaves per shoot (20 %), leaf area (28 %), SLA (25 %) and petiole length (44 %), were found in plants grown at high RH compared to moderate RH. Additionally, a 20 % decrease in internode length was found in plants grown at high RH plants compared to moderate RH. The number of side shoots on the main shoot showed a significant effect of UV, which resulted in a decreased number of side shoots in +UV plants compared to –UV plants. A weak effect of UV was found for both leaf area and petiole length, and a weak interaction between RH and UV was found for the number of leaves per shoot, all of which resulted in a slight decrease in +UV plants compared to –UV plants at both RH levels.

No significant effects of RH or UV on total biomass were found ($p > 0.1$, Figure 4). However, shoot DW distribution between stems and leaves showed that plants grown at high RH allocate ~15-20 % less DW to leaves than plants grown at moderate RH, with the result that plants grown at high RH had significantly higher stem DW than plants grown at moderate RH ($p = 0.0053$). A very weak effect of UV on stem DW ($p = 0.0915$) resulted in a slight decrease in stem biomass with exposure to UV compared to plants not exposed to UV in plants grown at both high and moderate RH. No effects of RH or UV were seen on leaf DW or total shoot DW.

Vegetative plants grown for 56 days are shown in Plate 1. +UV Plants grown at high RH (Plate 1d) show a slight discolouration of leaves, and –UV plants grown at high RH indicate a slight yellowing at the leaf tips, to a greater extent than plants grown at moderate RH with and without UV exposure.

Table 2. Effects of RH and UV radiation on morphological parameters of vegetative 'Christmas Feeling' Poinsettia (means ± SE, n = 5 for each treatment) grown for 56 days under LD conditions (20 h photoperiod). Plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV).

	60 % RH		90 % RH		Statistical Significance		
	-UV	+UV	-UV	+UV	RH	UV	RHxUV
Plant Height (cm)	14.70 ± 0.62	13.16 ± 1.04	17.00 ± 0.96	16.50 ± 0.91	**	NS	NS
Plant Diameter (cm)	27.05 ± 0.69	24.80 ± 1.11	29.40 ± 1.00	30.35 ± 1.34	**	NS	NS
Shoot Length (cm) ††	4.73 ± 0.17	4.13 ± 0.09	6.22 ± 0.46	6.49 ± 0.29	***	NS	NS
Leaves per Shoot †	11.25 [11.00-11.50]	9.75 [9.75-10.00]	12.50 [12.50-12.75]	12.25 [12.00-13.00]	**	NS	*
Leaf Area per leaf ($cm^{2)}$	11.96 ± 0.3	9.54 ± 0.63	14.92 ± 1.25	13.22 ± 1.10	**	*	NS
Plant SLA (cm^2 g^{-1}) †	182.90 [176.70-197.30	177.00 [170.60-219.70]	275.90 [245.60-292.10]	235.60 [233.90-245.90]	**	NS	NS
Side shoots on main shoot	7.60 ± 1.40	3.00 ± 1.05	7.40 ± 1.25	5.40 ± 1.86	NS	*	NS
Petiole Length (cm)	4.37 ± 0.36	3.25 ± 0.20	6.63 ± 0.40	5.76 ± 0.24	***	**	NS
Internode Length (cm)	2.38 ± 0.04	2.39 ± 0.05	1.87 ± 0.07	1.92 ± 0.08	***	NS	NS

Significance levels based on the overall effects of RH and UV radiation and RHxUV interaction as according to a two-way ANOVA or Kruskal-Wallis rank sum tests where data showed non-normality (†). Non-normal data presented as median [interquartile range (IQR)], interaction effects determined by Adjusted Rank Transform (ART) tests. †† Indicates heteroscedastic variables tested using One-Way Analyses of Means for main effects of each factor (on ART data for interaction effects).

Significance levels: NS, not significant ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

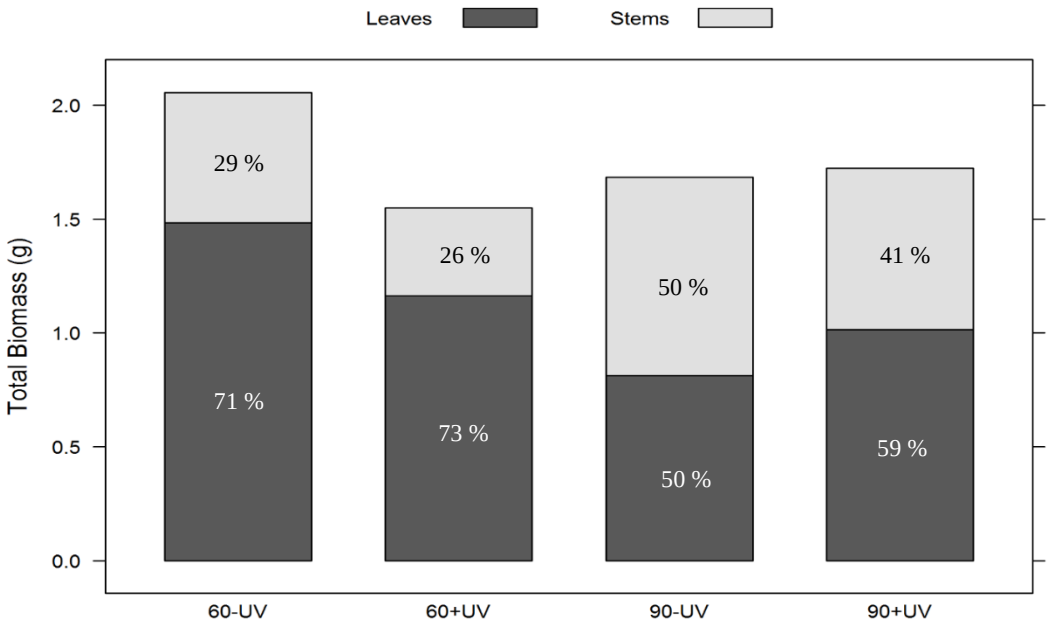


Figure 4. Total biomass (DW) and mean distribution of DW biomass between the leaves and the stem of the longest shoot on each plant for 'Christmas Feelings' Poinsettia plants grown in controlled growth chambers for 56 days under 20/4 h light/dark LD treatment. Plants were grown under one of two RH levels (60 % or 90 %) and either exposed (+UV) to 40 minutes daily of 0.15 W m^{-2} UV radiation given in the middle of the dark period or not (-UV). Dry weight as a percentage of total biomass is indicated for leaves and stems.

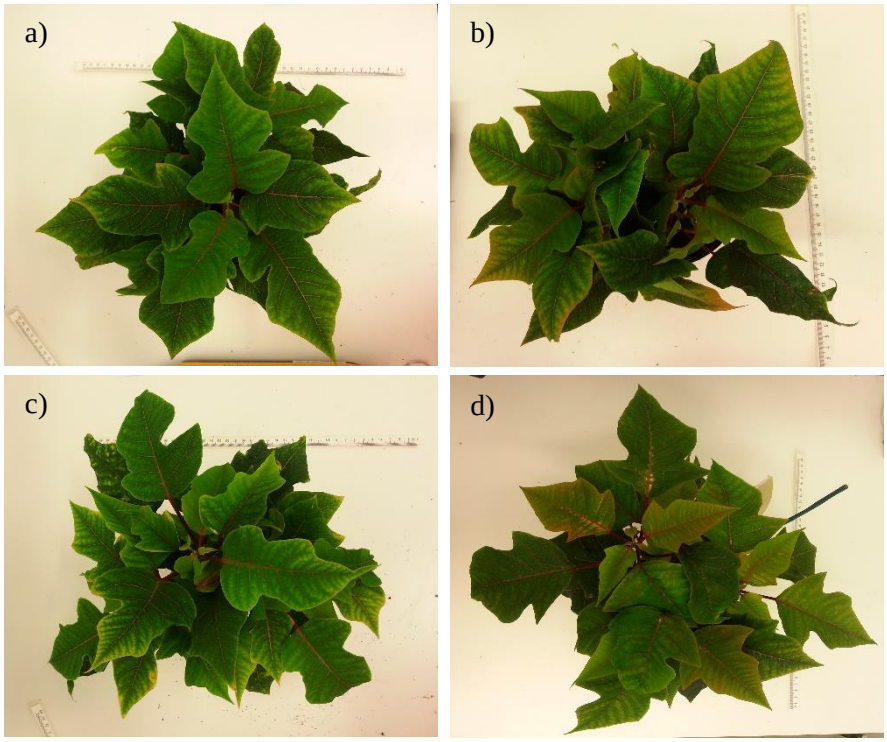


Plate 1. 'Christmas Feelings' poinsettia grown in growth chambers for 56 days under LD conditions. Plants were grown at one of two RH levels (60 % or 90 %) and either exposed (+UV) to 0.15 W m^{-2} UV radiation given in the middle of the dark period, or not (-UV). a) 60-UV plant, b) 60+UV plant, c) 90-UV plant and d) 90+UV plant.

Experiment 2: Generative growth of Poinsettia

Changes in shoot length of both 'Infinity Red' and 'Bravo Bright Red' plants (Figure 5) indicate effects of RH and UV radiation throughout shoot growth. In 'Infinity Red' plants (Figure 5a) shoots on plants grown at high RH were consistently longer than shoots on plants grown at moderate RH. From 28 days ASD the effects of UV exposure begin to show. 90+UV plants had an increased shoot length in comparison to 90–UV plants, yet the opposite is true in plants at moderate RH, where shoot length decreased slightly with exposure to UV radiation. 'Bravo Bright Red' plants (Figure 5b) show similar effects of RH, with high RH plants having consistently longer shoots, yet the increased shoot length in 90+UV plants occurs to a much smaller degree, while the decreased shoot length in 60+UV plants is slightly more exaggerated in this cultivar.

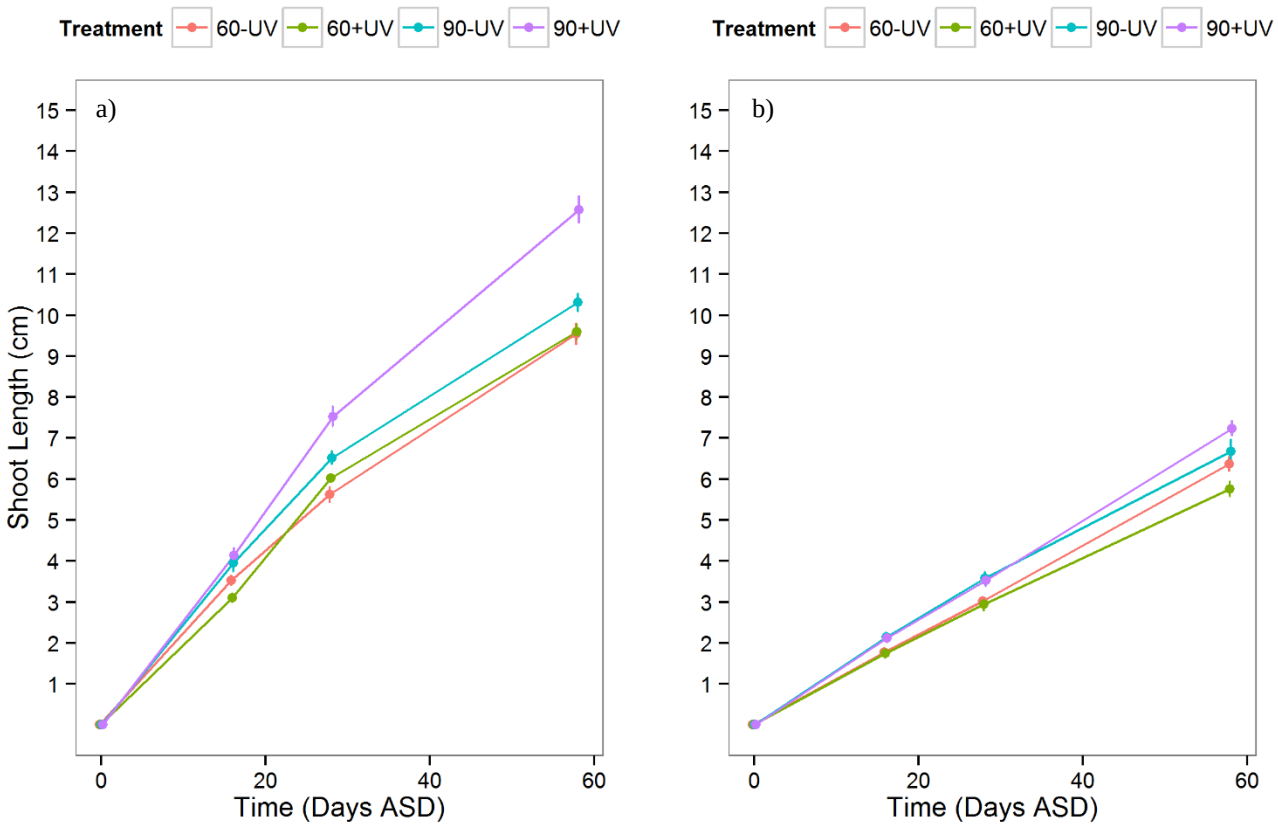


Figure 5. Growth curves showing average shoot length increase over time for the cultivars 'Infinity Red' (a) and 'Bravo Bright Red' (b) poinsettia grown for 58 days under 10/14 h light/dark SD treatment. The plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV). Points indicate average height of plants (n = 10 for each treatment) ± SE. Days ASD indicates the number of days after the start of SD treatment.

Plates 2 and 3 show ‘Infinity Red’ and ‘Bravo Bright Red’ plants respectively, grown for 28 days under SD conditions. +UV ‘Infinity Red’ plants grown at both moderate and high RH (Plate 2b and 2d respectively) show relatively severe leaf bronzing and leaf deformation compared to –UV plants (Plate 2a and 2c for moderate and high RH respectively), as well as a noticeable reduction in leaf area. Notably, -UV plants grown at high RH (Plate 2c) are slightly lighter in colour than leaves of the three other treatments.

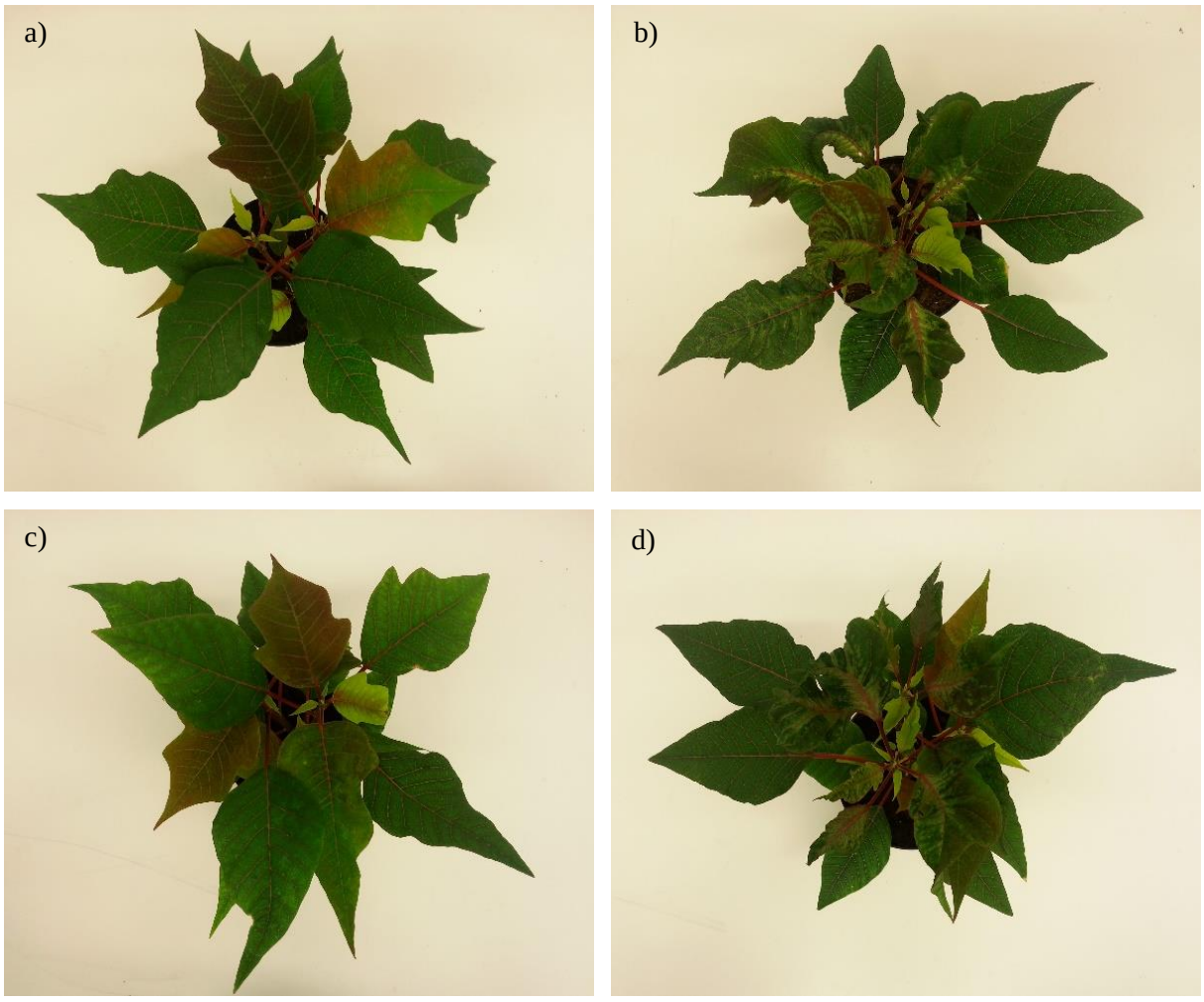


Plate 2. ‘Infinity Red’ poinsettia grown in growth chambers for 28 days under SD conditions. Plants were grown at one of two RH levels (60 % or 90 %) and either exposed (+UV) or not (-UV) to 0.15 W m^{-2} EOD UV radiation. a) 60-UV plant, b) 60+UV plant, c) 90-UV plant and d) 90+UV plant.

‘Bravo Bright Red’ plants (Plate 3) show similar effects of UV exposure to ‘Infinity Red’ plants, though to a slightly lesser extent. The leaves in +UV plants grown at both moderate RH (Plate 3b) and high RH (Plate 3d) indicate some bronzing and some deformation, though the decrease in leaf area compared to –UV plants is not as obvious as that seen in ‘Infinity Red’ plants. Leaves of –UV plants grown at high RH again indicate a slightly lighter colour than leaves of the other treatments.

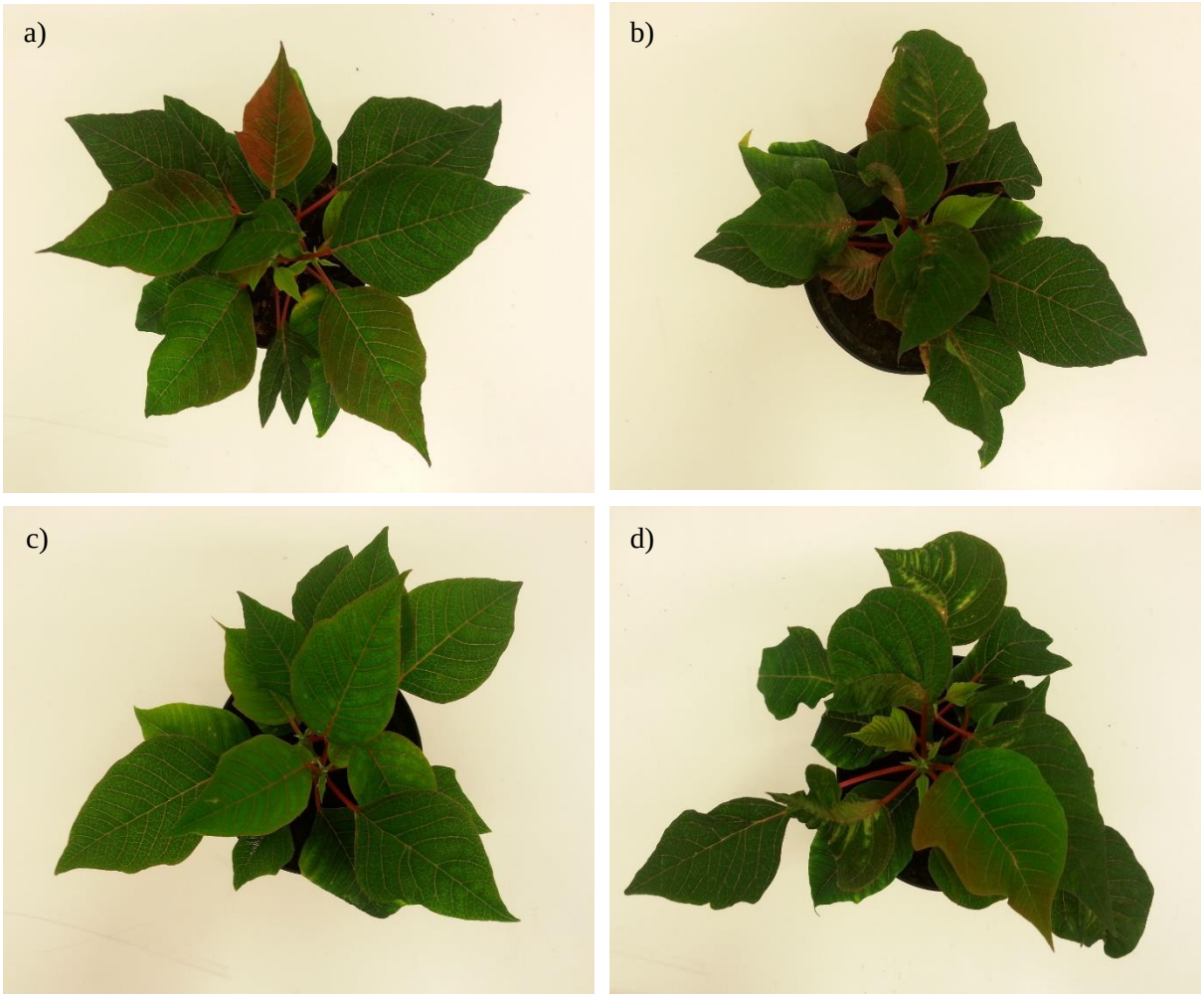


Plate 3. ‘Bravo Bright Red’ poinsettia grown in growth chambers for 28 days under SD conditions. Plants were grown at one of two RH levels (60 % or 90 %) and either exposed (+UV) or not (-UV) to 0.15 W m^{-2} EOD UV radiation. a) 60-UV plant, b) 60+UV plant, c) 90-UV plant and d) 90+UV plant.

Morphological parameters of 'Infinity Red' poinsettia

Plant height

Plant height of 'Infinity Red' was affected by RH and UV but no significant interaction was found between RH and UV (Table 3). The combination of high RH and UV exposure gave the tallest plants (~9 %). Shoot length, the number of leaves per stem and the number of bracts per stem were affected by an interaction between RH and UV (Table 3). The interaction of high RH and UV exposure gave the longest shoots (18-24 %), the highest number of leaves (14-19 %) and bracts (10-21 %) per shoot and the longest internodes (2-11 %) compared to the other treatments. The interaction between moderate RH and UV showed no effect on shoot length or the number of leaves per shoot, though it did result in a decrease in the number of bracts per shoot (21 %) and an increase in internode length (7.5 %) compared to –UV plants grown at moderate RH.

Plant diameter and other morphological parameters

A significant interaction effect dictated plant diameter in 'Infinity Red' plants, resulting in a similar pattern to that found in the number of bracts per stem, in that the direction and magnitude of the effects of UV were influenced by the RH level at which plants were grown (Table 3). An interaction effect between RH and UV was found for leaf and bract petiole lengths, leaf area and bract area. The interaction between high RH and UV resulted in an increase in both leaf (18 %) and bract (22 %) petiole lengths in comparison to -UV plants grown at high RH, though the plants grown at high RH had shorter leaf (20 %) and bract (22 %) petioles than the plants grown at moderate RH regardless of UV exposure. UV exposure combined with moderate RH resulted in no significant differences in leaf and bract petiole lengths between +UV and –UV plants at this RH level. The interaction effect on leaf area resulted in plants exposed to UV at both RH levels having decreased leaf area compared to plants not exposed to UV (38 % and 43 % for high and moderate RH respectively), and –UV plants grown at high RH had decreased leaf area compared to –UV plants grown at moderate RH (17 %). Bract area shows a similar effect of interaction to leaf and bract petiole lengths, in that the interaction between high RH and UV resulted in plants with a decreased bract area (8 %) compared to -UV high RH plants, yet plants grown at moderate RH had a higher bract area (29 %) than the plants grown at high RH regardless of UV exposure. Leaf and bract thickness (as SLA and SBA respectively) were both affected by RH and UV, though showed no effect of an interaction between RH and UV. For leaves the interaction between high RH and UV

resulted in the thickest leaves (6-15 %), and the interaction between moderate RH and UV resulted in an increase in leaf thickness (10 %) compared to –UV plants grown at moderate RH. In bracts the interaction between high RH and UV resulted in a decrease in bract thickness (19 %) compared to –UV plants grown at high RH, though plants grown at moderate RH had thinner bracts (16 %) than plants grown at high RH regardless of UV exposure. A one-day delay in visible cyathia was found for –UV plants grown at high RH (data not shown).

Shoot DW distribution

Shoot total DW was strongly affected by UV ($p < 0.0001$), which resulted in decreased shoot DW in +UV plants compared to -UV plants for plants grown at both levels of RH. Analyses of shoot DW distribution (Figure 6) indicate an effect of RH on the percentage of DW distributed to stems, resulting in a 42 % increase in the proportion of total DW allocated to stems in plants grown at high RH compared to plants grown at moderate RH. The opposite trend is seen in leaves and bracts, with an 8 % and 22 % decrease in DW proportion allocated to leaves and bracts respectively in plants grown at high RH compared to plants grown at moderate RH. No effects of UV were seen in shoot DW distribution. Shoot empirical DW shows a slightly more complicated story. Strong effects of both RH ($p < 0.0001$) and UV ($p < 0.0001$) on stem DW resulted in plants grown at high RH having increased stem DW compared to plants grown at moderate RH in addition to +UV plants having a decreased stem DW compared to –UV plants in plants grown at both levels of RH. A decrease in leaf DW in +UV plants compared to –UV plants in plants grown at both levels of RH is the result of a strong effect of UV on leaf DW ($p < 0.0001$). A strong interaction effect ($p = 0.0002$) on bract DW resulted in -UV plants grown at moderate RH showing significantly increased bract DW in comparison to all the other treatments, which showed no differences amongst themselves.

Table 3. Effects of RH and UV radiation on morphological parameters of generative 'Infinity Red' poinsettia (means ± SE, n = 10 for each treatment) grown for 58 days under 10/14 h light/dark SD treatment. Plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV).

	60 % RH		90 % RH		Statistical Significance		
	-UV	+UV	-UV	+UV	RH	UV	RHxUV
Plant Height (cm)	16.50 ± 0.5	16.90 ± 0.31	16.85 ± 0.40	18.45 ± 0.43	*	*	NS
Plant Diameter (cm)	36.60 ± 0.59	30.97 ± 0.49	31.20 ± 0.63	35.97 ± 1.03	NS	NS	***
Shoot Length (cm)	9.54 ± 0.27	9.59 ± 0.19	10.31 ± 0.22	12.57 ± 0.34	***	***	***
Leaves per Shoot	5.97 ± 0.19	5.60 ± 0.17	5.80 ± 0.13	6.93 ± 0.23	**	*	***
Bracts per shoot †	15.67 [15.42-16.25]	14.67 [14.67-15.16]	13.67 [13.33-14.00]	17.33 [16.50-18.16]	NS	*	***
Petiole Length Leaves (cm)	5.55 ± 0.14	5.51 ± 0.09	3.97 ± 0.11	4.85 ± 0.17	***	**	**
Petiole Length Bracts (cm)	2.98 ± 0.12	2.78 ± 0.06	1.96 ± 0.05	2.51 ± 0.15	***	NS	**
Internode Length (cm)	1.61 ± 0.19	1.72 ± 0.17	1.78 ± 0.13	1.82 ± 0.23	**	NS	NS
Leaf Area per Leaf (cm^2)	43.41 ± 1.23	24.43 ±1.17	35.97 ± 1.17	22.35 ± 0.97	***	***	*
Bract Area per Bract (cm^2)	36.12 ± 2.00	28.04 ± 1.03	21.76 ± 1.56	23.73 ± 1.38	***	▪	**
Plant SLA ($cm^2\ g^{-1}$)	271.19 ± 7.83	244.38 ± 5.83	248.81 ± 7.81	229.37 ± 4.01	**	**	NS
Plant SBA ($cm^2\ g^{-1}$)	414.90 ± 13.20	466.61 ± 15.19	331.22 ± 11.46	410.70 ± 11.16	***	***	NS
Chl Content Leaves	31.14 ± 1.56	40.21 ± 2.16	17.26 ± 0.86	29.12 ± 2.02	***	***	NS

Significance levels based on the overall effects of RH and UV radiation and RHxUV interaction as according to a two-way ANOVA or Kruskal-Wallis rank sum tests where data showed non-normality (†). Non-normal data presented as median [interquartile range (IQR)], interaction effects determined by Adjusted Rank Transform (ART) tests.

Significance levels: NS, not significant ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

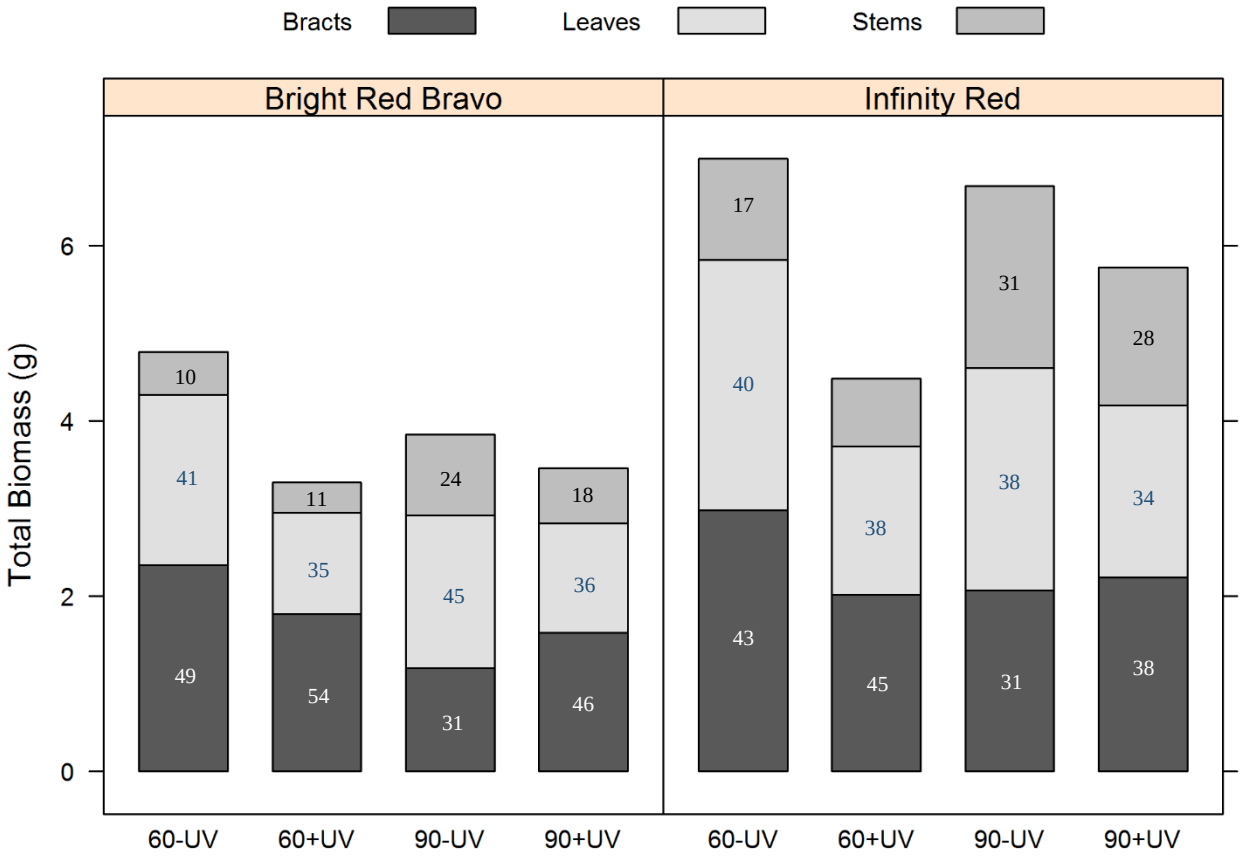


Figure 6. Distribution of dry weight biomass between leaves, bracts and stems (n = 10 for each treatment, n = 40 for each cultivar) for Poinsettia plants of 'Bravo Bright Red' and 'Infinity Red' cultivars, grown for 58 days under 10/14 h light/dark SD treatment. The plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV). Dry weight as a percentage of total biomass is indicated for leaves, bracts and stems separately.

Morphological parameters of 'Bravo Bright Red' poinsettia

Plant height

Neither plant height nor internode length in plants of the 'Bravo Bright Red' cultivar showed any effects of RH or UV (Table 4). The combination of high RH and UV resulted in plants with the longest shoots (8-20 %) and the greatest number of leaves per stem (6-18 %) compared to other treatments, however, the interaction effect between moderate RH and UV resulted in plants with shorter shoots (10 %) and fewer leaves (10 %) compared to –UV plants grown at the same RH level. The interaction effect between RH and UV on the number of bracts per shoot was relatively weak ($0.1 > p < 0.05$), and high RH combined with UV exposure resulted

in plants with a slightly higher number of bracts per shoot (5 %) compared to –UV high RH plants, though plants grown at moderate RH had more bracts per shoot (8 %) than plants grown at high RH regardless of UV exposure.

Plant diameter and other morphological parameters

'Bravo Bright Red' plant diameter, leaf and bract petiole lengths and leaf and bract areas were all affected by an interaction effect between RH and UV (Table 4). The interaction between high RH and UV resulted in an increase in diameter (4 %) compared to –UV plants grown at high RH, though in moderate RH plants the interaction between moderate RH and UV exposure resulted in a decrease in diameter (12 %) compared to –UV moderate RH plants. Petiole lengths of leaves and bracts show the same pattern to one another in that the combination of high RH and UV resulted in longer petioles (25 % and 41 % for leaves and bracts respectively) compared to –UV high RH plants, though plants grown at moderate RH had longer leaf (22 %) and bract (24 %) petioles than plants grown at high RH regardless of UV exposure. The interaction effect between RH and UV on leaf area showed the same effect on leaf area at high and moderate RH, where UV exposure resulted in a decrease (19 % and 39 % for high and moderate RH respectively) compared to –UV plants, and –UV plants grown at high RH had smaller leaves (21 %) than –UV plants grown at moderate RH. The combination of high RH and UV resulted in an increase in bract area (38 %) compared to –UV plants grown at high RH, while the combination of moderate RH and UV resulted in a decrease in bract area (9 %) compared to –UV plants grown at moderate RH. Additionally, plants grown at high RH had smaller bracts (33 %) than plants grown at moderate RH regardless of UV exposure. Leaf thickness was significantly affected by the interaction between RH and UV (Table 4), and the combination of high RH and UV resulted in a decrease in leaf thickness (17 %) compared to –UV high RH plants, while the combination of moderate RH and UV resulted in an increase in leaf thickness (6 %) compared to –UV moderate RH plants. Bract thickness was affected by RH and UV, with a weak interaction effect ($0.1 > p < 0.05$). UV exposure resulted in a decrease in bract thickness at both RH levels (21 % and 10 % for high and moderate RH respectively), while –UV plants grown at high RH had thicker bracts (40 %) than –UV plants grown at moderate RH. A one-day delay in visible cyathia was found for –UV plants grown at high RH (data not shown).

Shoot DW distribution

Plant total biomass was affected by an interaction between RH and UV ($p = 0.0249$, Figure 6), which resulted in –UV plants grown at moderate RH having the greatest shoot DW biomass. The distribution of DW to stems showed a significant effect RH and UV ($p < 0.0001$ for both). The combination of high RH and UV resulted in a slight decrease (6 %) in the proportion of DW allocated to stems compared to –UV high RH plants, though plants grown at high RH allocated approximately 50 % more DW to stems than plants grown at moderate RH. Leaf DW was affected solely by UV ($p < 0.0001$) and exposure to UV resulted in a decrease in the percentage of biomass allocated to leaves compared to –UV plants grown at both RH levels. Bract DW was affected by both RH and DW, though no interaction effect was seen between RH and UV. Exposure to UV resulted in an increase in the proportion of DW allocated to bracts compared to –UV plants at both RH levels (15 % and 6 % for high RH and moderate RH respectively), though the plants grown at high RH allocated 13 % less DW to bracts compared to moderate RH plants. Empirically, the combination of high RH and UV resulted in a decrease in stem DW compared to –UV high RH plants, while no significant difference in stem DW was seen between +UV and –UV plants grown at moderate RH. The significant effect of UV on leaf DW resulted in a decrease in leaf DW in +UV plants compared to –UV plants grown at both levels of RH. The combination of high RH and UV resulted in an increase in bract DW in comparison to –UV high RH plants, yet the combination of moderate RH and UV resulted in a decrease in bract DW compared to –UV moderate RH plants. Additionally, plants grown at high RH had lower bract DW than plants grown at moderate RH regardless of UV exposure.

Table 4. Effects of RH and UV radiation on morphological parameters of generative 'Bright Red Bravo' poinsettia (means ± SE, n = 10 for each treatment) grown for 58 days under 10/14 h light/dark SD treatment. Plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV).

	60 % RH		90 % RH		Statistical Significance		
	-UV	+UV	-UV	+UV	RH	UV	RHxUV
Plant Height (cm)	10.65 ± 0.41	10.10 ± 0.41	9.95 ± 0.35	10.20 ± 0.35	NS	NS	NS
Plant Diameter (cm)	33.97 ± 0.79	29.77 ± 0.89	27.80 ± 1.03	28.95 ± 1.10	***	NS	**
Shoot Length (cm)	6.37 ± 0.18	5.75 ± 0.18	6.67 ± 0.29	7.24 ± 0.20	***	NS	*
Leaves per Shoot	14.50 [14.00-15.00]	13.00 [13.00-14.75]	15.00 [13.00-15.75]	16.00 [14.25-16.00]	*	NS	*
Bracts per Shoot	11.30 ± 0.28	10.53 ± 0.24	9.77 ± 0.44	10.30 ± 0.29	**	NS	▪
Petiole Length Leaves (cm)	5.94 ± 0.16	5.24 ± 0.15	3.70 ± 0.11	4.95 ± 0.12	***	▪	***
Petiole Length Bracts (cm)	3.72 ± 0.16	3.20 ± 0.15	1.94 ± 0.11	3.31 ± 0.17	***	**	***
Internode Length (cm)	3.83 ± 0.50	2.41 ± 0.48	3.05 ± 0.74	3.34 ± 0.51	NS	NS	NS
Leaf Area per Leaf (cm^2)	33.72 ± 1.35	20.63 ± 1.11	26.74 ± 1.75	21.70 ± 0.90	*	***	**
Bract Area per Bract (cm^2)	29.13 ± 1.07	26.45 ± 1.38	14.30 ± 1.39	22.96 ± 1.42	***	*	***
Plant SLA (cm^2 g^{-1}) †	249.20 [244.60-253.40]	234.10 [227.20-243.10]	217.50 [198.60-227.60]	263.30 [261.20-271.00]	NS	▪	***
Plant SBA (cm^2 g^{-1})	421.61 ± 11.38	470.89 ± 9.69	351.03 ± 19.01	446.11 ± 10.97	***	***	▪
Chl Content Leaves	39.18 ± 2.75	44.37 ± 2.32	23.98 ± 2.57	35.34 ± 3.22	***	**	NS

Significance levels based on the overall effects of RH and UV radiation and RHxUV interaction as according to a two-way ANOVA or Kruskal-Wallis rank sum tests where data showed non-normality (†). Non-normal data presented as median [interquartile range (IQR)], interaction effects determined by Adjusted Rank Transform (ART) tests.

Significance levels: NS, not significant ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Plate 4 shows ‘Infinity Red’ plants on the day of harvest, 58 days ASD. Visible leaf damage is seen on the leaves of +UV plants grown at moderate RH (Plate 4b). Some bract curling is seen in +UV plants grown at both moderate (Plate 4b) and high (Plate 4d) RH.

Plate 4. ‘Infinity Red’ poinsettia grown in growth chambers for 58 days under SD conditions. Plants were grown at one of two RH levels (60 % or 90 %) and either exposed (+UV) or not (-UV) to 0.15 W m^{-2} EOD UV radiation. a) 60-UV plant, b) 60+UV plant, c) 90-UV plant and d) 90+UV plant.

Plate 5 shows ‘Bravo Bright Red’ plants on the day of harvest, 58 days ASD. Similarly to ‘Infinity Red’ plants, +UV plants grown at moderate RH (Plate 5b) show the most obvious signs of leaf damage, including leaf bronzing and deformation. Notably, the leaves of the –UV plant grown at high RH are lighter than those of the other treatments, and the same plant shows a distinct decrease in the number of visible bracts.

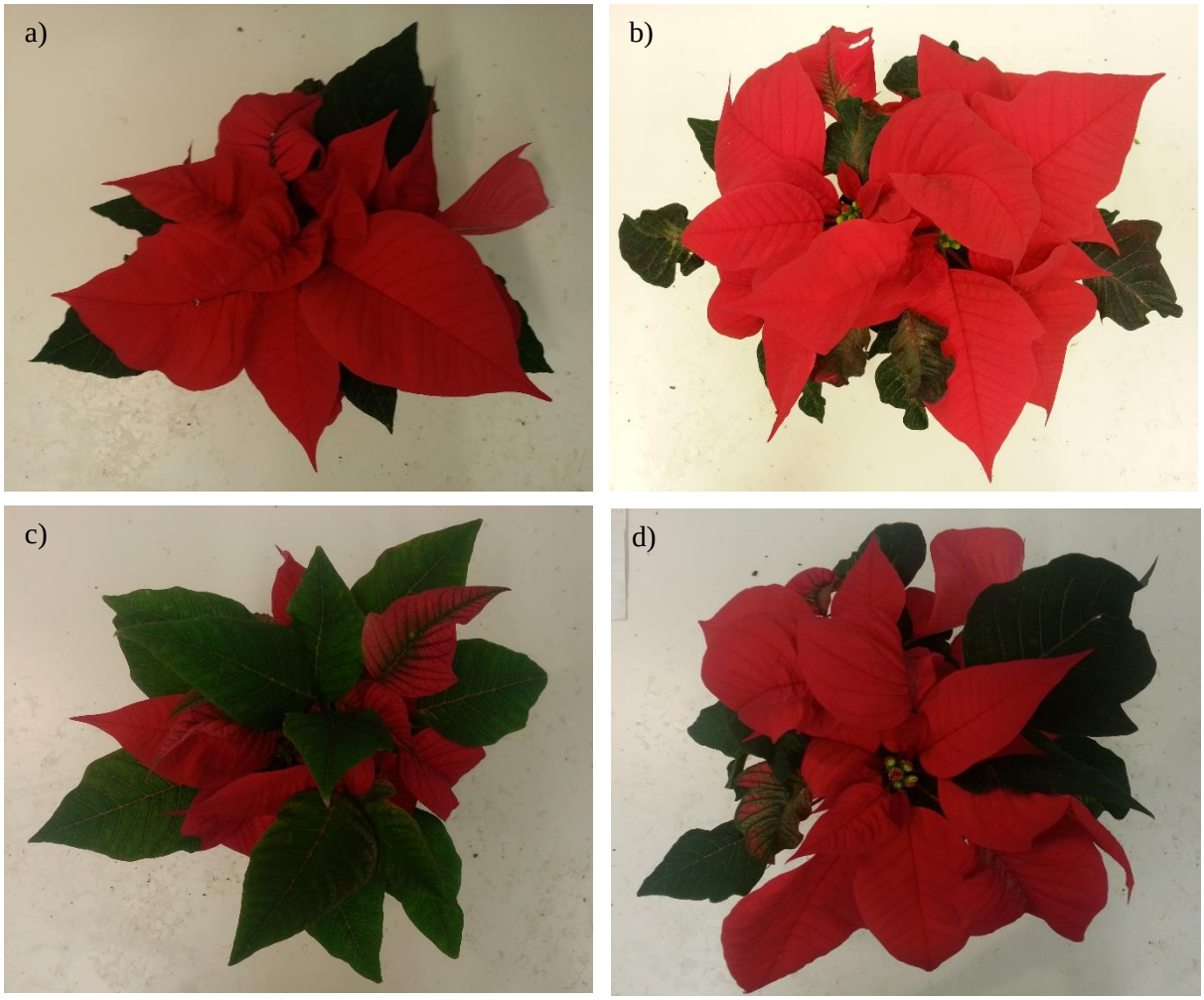


Plate 5. ‘Bravo Bright Red’ poinsettia grown in growth chambers for 58 days under SD conditions. Plants were grown at one of two RH levels (60 % or 90 %) and either exposed (+UV) or not (-UV) to 0.15 W m^{-2} EOD UV radiation. a) 60-UV plant, b) 60+UV plant, c) 90-UV plant and d) 90+UV plant.

Stomatal parameters of 'Infinity Red' plants

Stomatal responses to UV and RH in 'Infinity Red' poinsettia grown in short day conditions and measured in the light are shown in Table 5. A 7 % and an 11 % increase in stomatal aperture size measured in the light was seen in +UV plants compared to –UV plants grown at high and moderate RH respectively. When measured in the dark stomatal aperture size is significantly affected by RH, resulting in a 24 % increase in aperture size in plants grown at high RH compared to plants grown at moderate RH. A weak effect of UV and a weak interaction effect further result in a 16 % increase in aperture size in +UV plants grown at high RH compared to –UV plants, though no differences were found in response to UV exposure in plants grown at moderate RH. Leaf stomatal conductance (Table 5) measured on plants outside the chambers (40-50 % RH) showed a strong effect of RH, resulting in a 44 % increase in stomatal conductance in plants grown at high RH compared to plants grown at moderate RH. The same parameters measured in the dark (Table 5) showed more varied responses due to an interaction effect between RH and UV. The combination of RH and UV resulted in a decrease in conductance in +UV plants compared to –UV plants at both RH levels (30 % and 9 % for high RH and moderate RH respectively). Additionally, plants grown at high RH showed a 67 % increase in conductance compared to plants grown at moderate RH. Neither RH nor UV had an effect on bract conductance measured in light conditions (Table 5), though when measured in the dark an interaction between RH and UV determined bract conductance in the dark. The combination of high RH and UV resulted in a 61 % decrease in bract conductance compared to –UV high RH plants, while the combination of UV and moderate RH resulted in a 17 % decrease in bract conductance compared to –UV moderate RH plants. Additionally, bract conductance in high RH plants was 68 % higher than that in moderate RH regardless of UV exposure. Notably, in plants grown at high RH bract conductance was 43 % higher under dark conditions than under light conditions.

Figure 7 illustrates differences in stomatal aperture size between light and dark conditions for all treatments. Compared to light conditions, the effect of darkness on plants grown at moderate RH resulted in 31 % and 24 % decreases respectively in stomatal aperture size in +UV and –UV plants. However, compared to light conditions the effect of darkness on plants grown at high RH resulted in a mere 8 % decrease in stomatal aperture size in plants not exposed to UV, while resulting in a 2 % increase in plants exposed to UV.

Table 5. Effects of RH and UV radiation on stomatal aperture size, leaf and bract conductance and leaf photosynthesis (means ± SE, *n* = 10 for each treatment of leaf and bract conductance and photosynthesis; *n* for aperture size shown in table) of generative 'Infinity Red' poinsettia grown for (58) days under 10/14 h light/dark SD treatment and measured under both light and dark conditions. Plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed to 0.15 W m^{-2} for 40 minutes EOD UV radiation (+UV) or not (-UV). Aperture size and photosynthesis measurements took place inside the growth chambers, while plants were removed from the chambers for conductance measurements.

	60 % RH		90 % RH		Statistical Significance		
	-UV	+UV	-UV	+UV	RH	UV	RH*UV
Light							
Stomatal Aperture Size (µm) †	3.69 [3.08-4.26] (*n* = 70)	4.13 [3.38-4.63] (*n* = 84)	3.68 [3.12-4.18] (*n* = 78)	3.94 [3.38-4.68] (*n* = 87)	NS	***	NS
Leaf Conductance (µmol m^{-2} s^{-1})	202.60 ± 18.61	198.70 ± 14.18	349.30 ± 16.74	363.60 ± 24.58	***	NS	NS
Bract Conductance (µmol m^{-2} s^{-1})	21.64 ± 1.90	18.10 ± 1.94	23.80 ± 3.00	22.34 ± 1.54	NS	NS	NS
Photosynthesis (µmol m^{-2} s^{-1})	5.52 ± 0.17	5.20 ± 0.20	5.29 ± 0.18	5.23 ± 0.17	NS	NS	NS
Dark							
Stomatal Aperture Size (µm) †	2.79 [2.43-3.27] (*n* = 80)	2.82 [2.42-3.51] (*n* = 74)	3.38 [2.85-4.43] (*n* = 128)	4.03 [3.33-4.76] (*n* = 87)	***	▪	*
Leaf Conductance (µmol m^{-2} s^{-1}) ††	39.50 ± 2.55	35.80 ± 3.37	134.90 ± 9.81	94.80 ± 11.46	***	NS	**
Bract Conductance (µmol m^{-2} s^{-1})	10.20 ± 0.48	8.50 ± 0.52	41.60 ± 1.08	16.04 ± 3.56	***	***	***

Significance levels based on the overall effects of RH and UV radiation and RHxUV interaction as according to a two-way ANOVA or Kruskal-Wallis rank sum tests where data showed non-normality (†). Non-normal data presented as median [interquartile range (IQR)], interaction effects determined by Adjusted Rank Transform (ART) tests. †† Indicates heteroscedastic variables tested using One-Way Analyses of Means for main effects of each factor (on ART data for interaction effects).

Significance levels: NS, not significant ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 6. Effects of RH and UV radiation on leaf and bract conductance and leaf photosynthesis (means ± SE, n = 10 for each treatment) of generative 'Bright Red Bravo' poinsettia grown for (X) days under 10/14 h light/dark SD treatment and measured under both light and dark conditions. Plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed to 0.15 W m^{-2} for 40 minutes EOD UV radiation (+UV) or not (-UV). Photosynthesis measurements took place inside the growth chambers, while plants were removed from the chambers for conductance measurements.

	60 % RH		90 % RH		Statistical Significance		
	-UV	+UV	-UV	+UV	RH	UV	RH*UV
Light							
Leaf Conductance (µmol m^{-2} s^{-1}) ††	292.40 ± 16.87	254.10 ± 17.71	443.20 ± 60.14	522.00 ± 24.58	***	NS	NS
Bract Conductance (µmol m^{-2} s^{-1})	22.08 ± 2.10	18.64 ± 2.41	32.90 ± 3.06	40.08 ± 1.54	***	NS	NS
Photosynthesis (µmol m^{-2} s^{-1})	5.06 ± 0.11	5.06 ± 0.22	4.94 ± 0.20	5.27 ± 0.08	NS	NS	NS
Dark							
Leaf Conductance (µmol m^{-2} s^{-1}) ††	22.60 ± 2.75	21.60 ± 3.23	94.60 ± 9.41	98.10 ± 12.67	***	NS	*
Bract Conductance (µmol m^{-2} s^{-1})	10.22 ± 0.22	10.34 ± 0.64	16.24 ± 2.12	15.54 ± 3.65	*	NS	NS

Significance levels based on the overall effects of RH and UV radiation and RHxUV interaction as according to a two-way ANOVA. †† Indicates heteroscedastic variables tested using One-Way Analyses of Means for main effects of each factor (on Adjusted Rank Transformed data for interaction effects).

Significance levels: NS, not significant ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

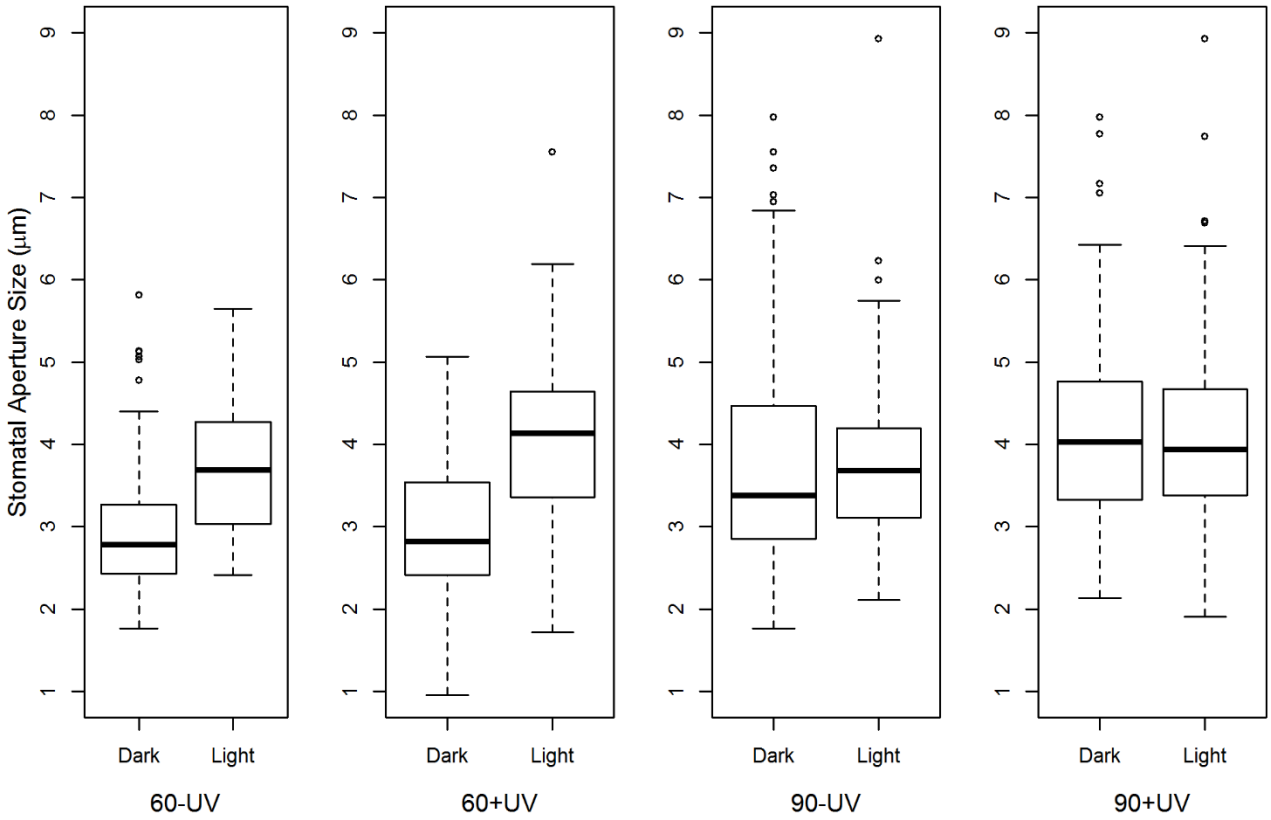


Figure 7. Stomatal aperture size of four treatments (n > 70 for each treatment) during growth of 'Infinity Red' poinsettia grown for 58 days under 10/14 h light/dark SD treatment and measured both in the middle of the light period and 1 h into the dark period. The plants were grown in growth chambers under one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV).

Transpiration of 'Bravo Bright Red' plants

Leaf and bract conductance of 'Bravo Bright Red' plants measured in light conditions and bract conductance measured in dark conditions were solely affected by RH (Table 6). In light conditions this resulted in 43 % higher leaf conductance in plants grown at high RH compared to plants grown at moderate RH and 44 % higher bract conductance in plants grown at high RH compared to plants grown at moderate RH. In dark conditions an interaction between RH and UV affected leaf conductance, though this interaction resulted in minor differences between +UV and –UV plants. There was, however, a 77 % increase in leaf conductance in plants grown at high RH compared to moderate RH. Bract conductance in dark conditions was affected solely by RH, which resulted in a 35 % increase in bract conductance in plants grown at high RH compared to moderate RH.

Plates 6 and 7 show stomata of leaves and bracts from all four treatments, photographed at 3000x magnification under a scanning electron microscope (SEM). Due to preservation conditions no differences in aperture sizes can be seen in leaf stomata (Plate 1), all of which appear to be closed. Bract stomata (Plate 2) are less conspicuous and seem to be covered in a thin cuticular wax layer. Notably, bract stomata were few and far between and difficult to find under the microscope, though it was beyond the scope of this project to determine stomatal density using SEM.

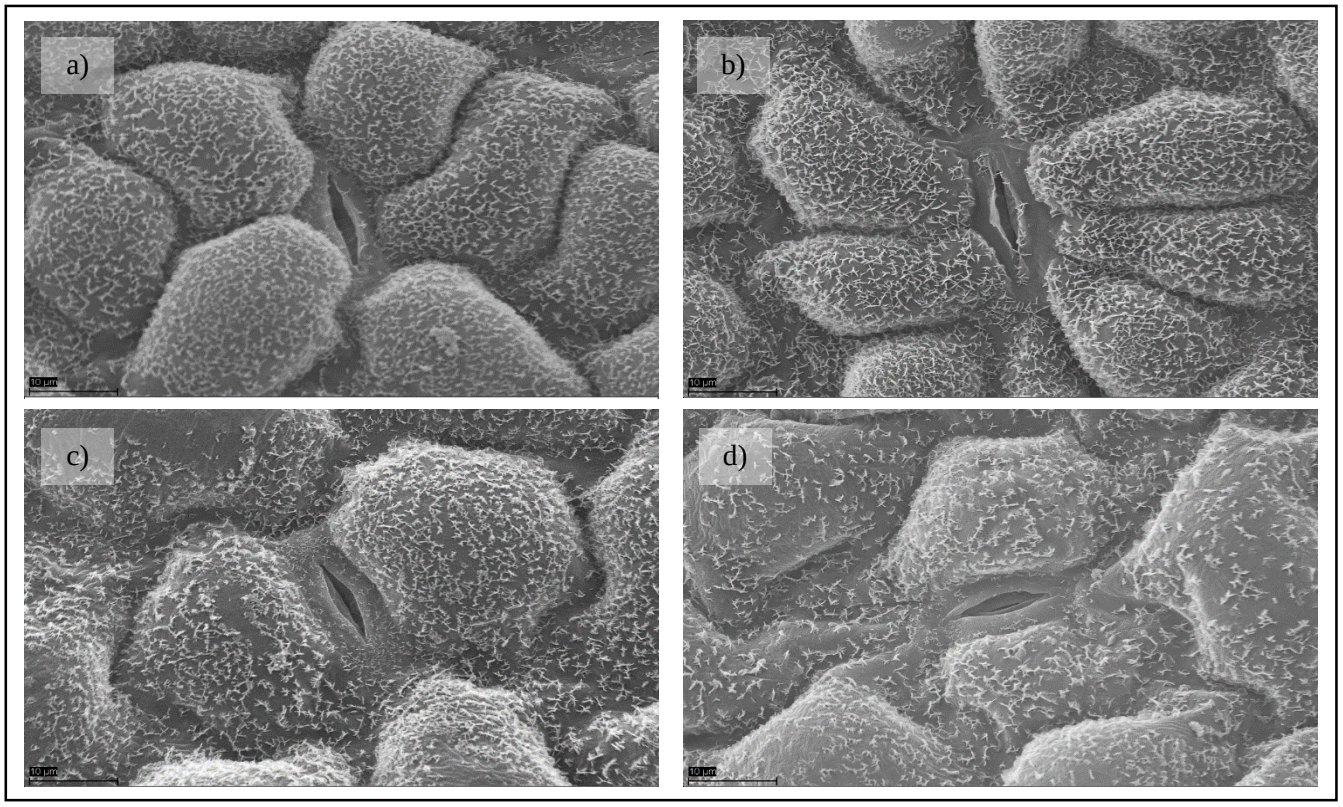


Plate 6. Leaf stomata from the lower side of the leaves taken at 3000x magnification using SEM, a) 60-UV leaf, b) 90-UV leaf, c) 60+UV leaf, d) 90+UV leaf.

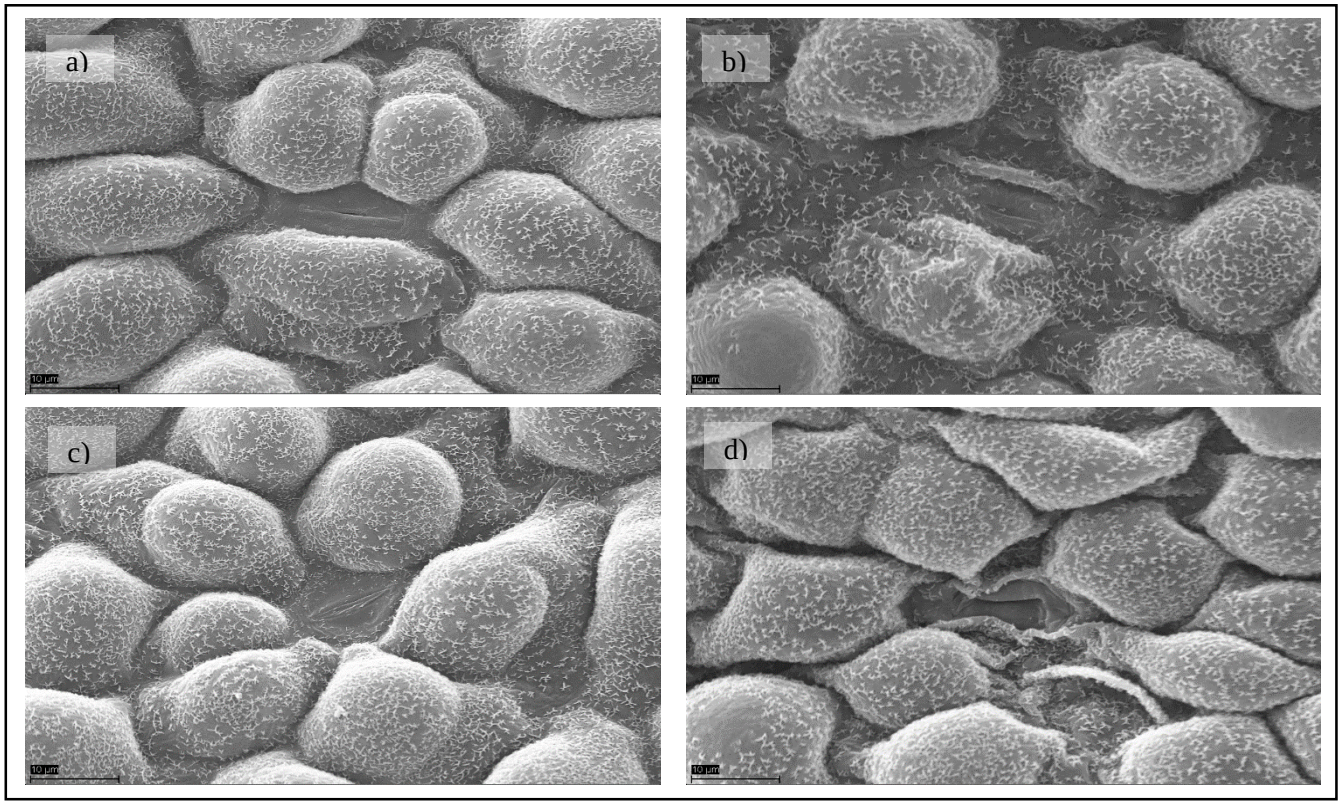


Plate 7. Bract stomata from the lower side of the bracts taken at 3000x magnification using SEM, a) 60-UV bract, b) 90-UV bract, c) 60+UV bract, d) 90+UV bract.

Experiment 3: Generative growth of poinsettia in a greenhouse

Morphological parameters

Growth and morphology of 'Christmas Day' Poinsettia grown in short day conditions was significantly affected by UV radiation (Table 7). Plant height and plant diameter showed respectively a 16 % and 7 % reduction in +UV plants compared to –UV plants. Similarly, reductions in shoot length (9 %), internode length (13 %), leaf area (28 %), bract area (16 %), SLA (19 %) and SBA (9 %) were found in plants exposed to UV compared to plants not exposed to UV. Additionally, a 16 % increase in bract anthocyanin content in +UV plants compared to –UV plants was found. UV radiation had no significant effect on the number of leaves or bracts per shoot or leaf petiole length.

Table 7. Effects of UV radiation on morphological parameters of generative 'Christmas Day' Poinsettia (means ± SE, n = 10 for each treatment) grown for 63 days under 10/14 h light/dark SD treatment. Plants were grown in a greenhouse compartment and either exposed for 7.5 minutes to 0.80 W m^{-2} EOD UV radiation (+UV) or not (-UV).

	Treatment		Statistical Significance
	-UV	+UV	UV
Height (cm)	17.20 ± 0.53	14.50 ± 0.25	***
Diameter (cm)	37.75 ± 0.47	35.15 ± 0.55	**
Shoot Length (cm)	12.73 ± 0.40	11.60 ± 0.16	*
Leaves per Shoot	5.13 ± 0.10	5.39 ± 0.12	NS
Bracts per Shoot †	11.33 [10.75-11.33]	10.67 [10.42-10.92]	NS
Petiole Length Leaves (cm)	6.26 ± 0.24	6.06 ± 0.13	NS
Internode Length (cm)	2.48 ± 0.07	2.16 ± 0.05	**
Leaf Area per leaf (cm^2)	47.04 ± 0.92	33.62 ± 0.93	***
Bract Area per bract (cm^2)	47.86 ± 1.67	40.12 ± 0.92	***
Plant SLA (cm^2 g^{-1})	136.95 ± 2.25	111.39 ± 2.64	***
Plant SBA (cm^2 g^{-1})	254.25 ± 3.94	230.79 ± 4.50	***
Anthocyanin Content (mmol m^{-2})	1.36 ± 0.07	1.62 ± 0.04	*

Significance levels based on the overall effects of RH and UV radiation and RHxUV interaction as according to a two-way ANOVA or Kruskal-Wallis rank sum tests where data showed non-normality (†). Non-normal data presented as median [interquartile range (IQR)], interaction effects determined by Adjusted Rank Transform (ART) tests.

Significance levels: NS, not significant (p < 0.1); ▪ p < 0.1; * p < 0.05; ** p < 0.01; *** p < 0.001

Exposure to UV radiation had a significant effect on plant total DW (p = 0.0195), which showed a significant decrease in plants exposed to UV radiation compared to plants not exposed to UV radiation (Figure 8). The shoot DW distribution in plants of both treatments was found to be the same (Figure 8), with plants of both treatments allocating 25 % of total DW to stems, 35 % to leaves and 40 % to bracts. While proportionally the DW distribution shows no difference, there was a significant difference in empirical DW between treatments in all three of stems, leaves and bracts, with plants exposed to UV radiation showing a significant reduction in these parameters compared to plants not exposed to UV radiation (p = 0.0107, p = 0.0280 and p = 0.0415 for leaves, bracts and stems respectively).

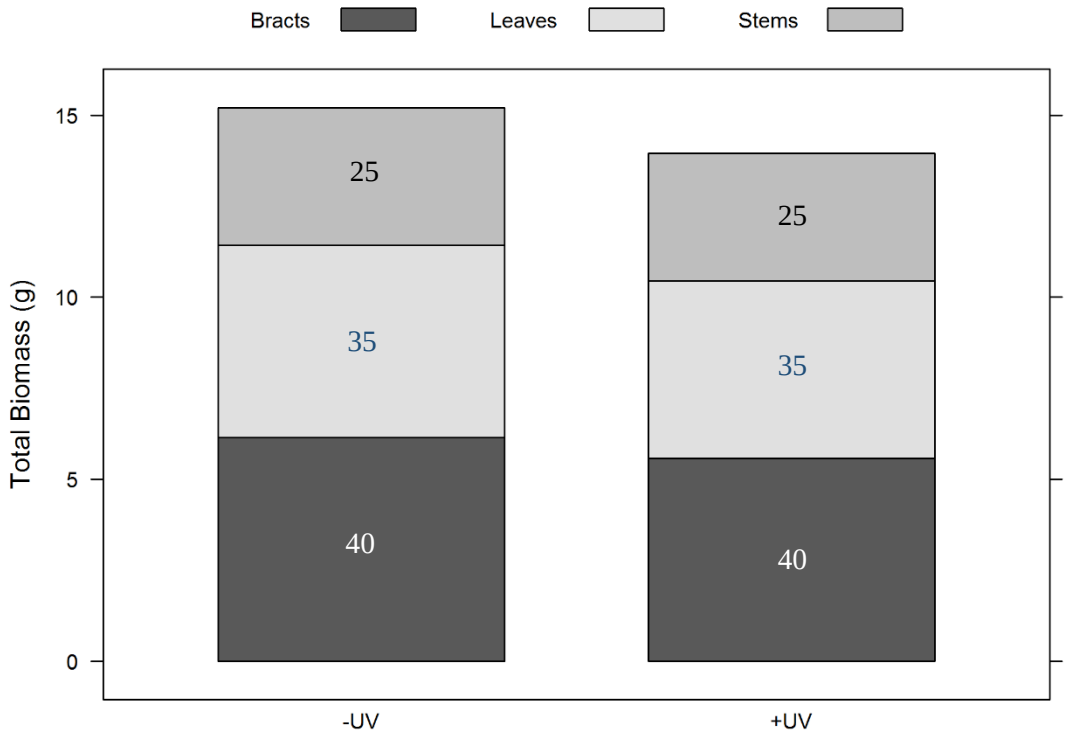


Figure 8. Distribution of dry weight biomass between leaves, bracts and stems (n = 10 for each treatment) for generative 'Christmas Day' Poinsettia, grown for 63 days under 10/14 h light/dark SD treatment. The plants were grown in a greenhouse compartment and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV). Dry weight as a percentage of total biomass is indicated for leaves, bracts and stems separately.

Plate 8 shows 'Christmas Day poinsettia on the day of harvest, 63 days ASD. The decrease in height in +UV plants compared to –UV plants is visible.

Light response curve

No significant effects of UV radiation were found on photosynthetic CO_2 assimilation (Figure 9a) under increasing light intensity, yet exposure to UV radiation resulted in a trend towards increased rates of both transpiration (Figure 9b) and stomatal conductance (Figure 9c) in plants compared to plants not exposed to UV radiation. The trend was weakly significant at 25 %, 10 %, 5 % and 0 % of total irradiance in transpiration rate (p = 0.0.0514, p = 0.0469, p = 0.0418, p = 0.0358 respectively), though no significant differences were found at any irradiance for stomatal conductance. Notably, both transpiration and stomatal conductance rates in +UV plants show a slight decrease between total darkness and 2.5 % of saturating light intensity.

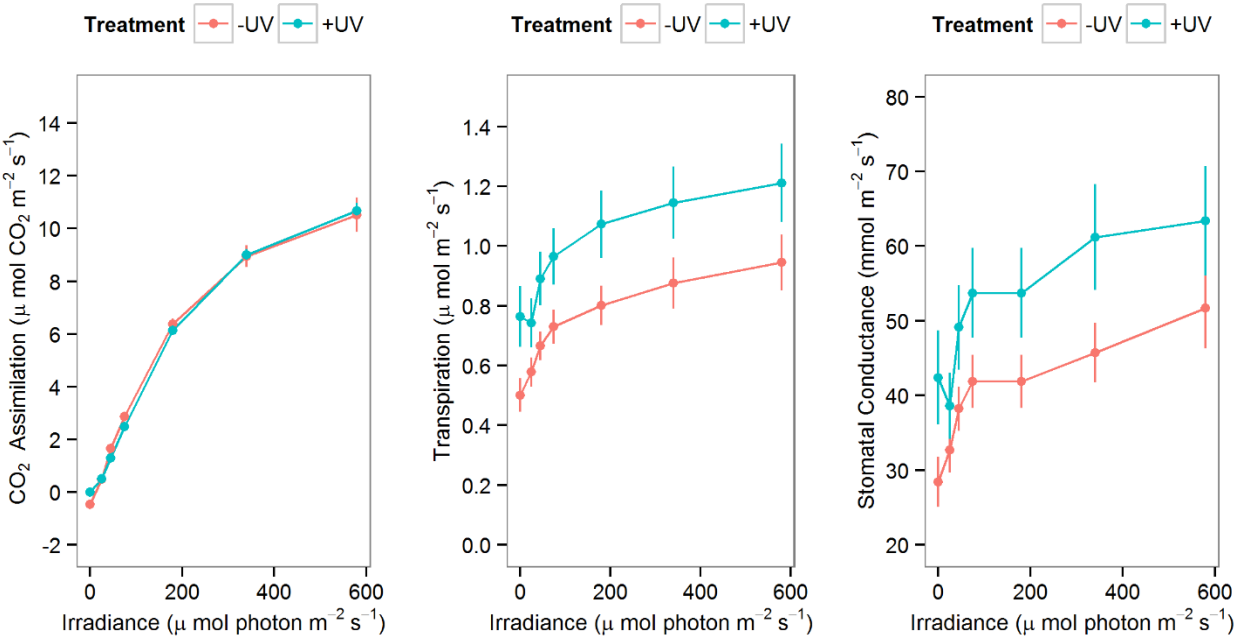


Figure 9. Response curves of a) CO_2 assimilation rate (photosynthesis), b) transpiration rate and c) rate of stomatal conductance of green leaves to increasing irradiance levels in generative 'Christmas Day' Poinsettia, grown for 63 days under 10/14 h light/dark SD treatment. The plants were grown in a greenhouse compartment and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV). Points indicate average values ± SE.

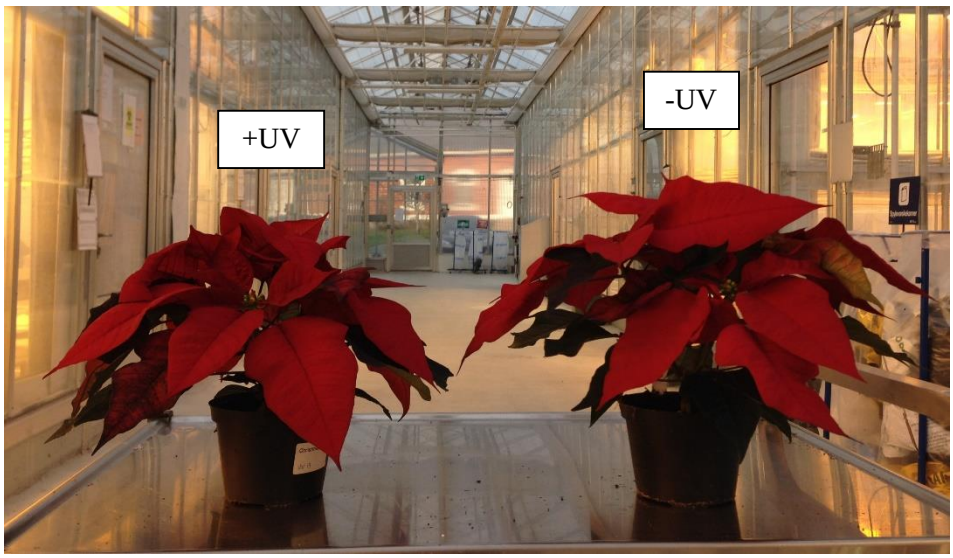


Plate 8. 'Christmas Day' poinsettia grown in a greenhouse for 63 days under SD conditions. Plants were grown at 70 % RH and either exposed (+UV) to 0.15 W m^{-2} EOD UV radiation, or not exposed (-UV).

Discussion

Growth and morphological responses to air humidity and UV radiation

Morphological responses of plants to UV radiation have been investigated for several decades, with the most common responses being a reduction in plant height, reduced plant biomass, smaller, thicker leaves with reduced biomass, a reduction in chlorophyll content, changes in epicuticular wax content and in cases of UV-induced damage, leaf bronzing (Ballare et al. 1996; Baroniya et al. 2011; Barsig & Malz 2000; Cen & Bornman 1990; Deckmyn & Impens 1998; Deckmyn & Impens 1999; Gehrke et al. 1996; Grammatikopoulos et al. 1998; Johanson et al. 1995; Kakani et al. 2003; Koti et al. 2007; Lingakumar et al. 1999; Liu et al. 1995; Mackerness et al. 1998; Meijkamp et al. 2001; Nedunchezhian & Kulandaivelu 1997; Nogués et al. 1998; Qaderi et al. 2008; Rozema et al. 2006; Singh et al. 2012; Surabhi et al. 2009). The detrimental effects of UV radiation on leaf growth is a well-documented response in plants of numerous species (Cen & Bornman 1990; Frohnmeyer & Staiger 2003; Liu et al. 1995; Wargent et al. 2009). However, it should be noted that in several studies the detrimental effects of UV radiation on leaf growth were found to be dose-dependent (Cen & Bornman 1990; Lydon et al. 1986; Wargent et al. 2009), as well as dependent on background PAR levels, with low level background PAR often causing increased sensitivity to UV radiation (Cen & Bornman 1990; Liu et al. 1995; Teramura & Sullivan 1994). Morphological responses to changes in RH are generally more uniform than those induced by UV radiation, with most studies showing agreement in the responses found, albeit to differing degrees, though that is not to say that anomalous results have not been found. For instance, in six studies that mention responses to RH on shoot length in their analyses (Hoffman et al. 1971; Mortensen 1986; Mortensen & Fjeld 1998; Mortensen & Gislerød 1999; Mortensen 2000; Torre & Fjeld 2001), four reported increased shoot length as a response to increased RH (Hoffman et al. 1971; Mortensen 1986; Mortensen & Fjeld 1998; Mortensen 2000), while Torre and Fjeld (2001) found negligible effects on plant height, and Mortensen and Gislerød (1999) found a decrease in shoot length in all 14 rose cultivars examined at high RH. Leaf morphological responses to increased RH include increases in leaf area (Hovenden et al. 2012; Leuschner 2002; Mortensen 2000) and the total number of leaves (Mortensen 1986), leaf thickening (Hovenden et al. 2012), leaf thinning (Torre et al. 2003) and a decrease in cuticular wax (Kerstiens 1994; Koch et al. 2006).

Growth and morphological responses to combinations of RH and UV radiation were tested in vegetative 'Christmas Feelings' and generative 'Infinity Red' and 'Bravo Bright Red' poinsettia plants grown in controlled environment growth chambers between December 2013 and July 2014. Additionally, growth and morphological responses of generative 'Christmas Day' poinsettia to UV radiation alone were tested in plants grown in a greenhouse compartment between September and December in 2014. The time period and greenhouse environmental conditions of Experiment 3 (excluding UV radiation) were set to mimic those of commercial poinsettia production in Norway. In all experiments UV induced changes in morphology, however, the effect of UV was dependent on ontogenetic stage, background air humidity and cultivar.

Whole-plant morphology

In this study vegetative 'Christmas Feelings' plants (Experiment 1) in general showed a stronger growth response to RH than to UV radiation, with plants grown at 90 % RH being significantly taller and wider (diameter), and having a greater number of larger, thinner leaves with longer petioles and shorter internodes, than plants grown at 60 % RH, regardless of UV exposure. The number of side shoots on the main shoot singularly showed no response to RH, with UV exposure resulting in a decrease in the number of side shoots compared to –UV plants at both RH levels. Both leaf area and leaf petiole length showed responses to UV in addition to RH. UV exposure reduced both parameters relative to -UV plants at both RH levels. Aasamaa and Sober (2011) found that in six species of temperate deciduous trees the responses in stomatal conductance to changes in hydraulic environmental factors (leaf water potential and RH) dominated unanimously over simultaneous changes in photosynthetic environmental factors (CO_2 concentration and light intensity). They postulated that this stronger response to hydraulic environmental factors stems from the greater importance of maintaining water balance for the survival of the plant. Their postulation may have grounds in the morphological responses to environmental factors in vegetative plants reported here, given that during the vegetative phase survival and growth are of utmost importance, whereas in the generative phase it is the promotion of flowering and reproduction that govern responses.

Generative plants showed a stronger response to UV radiation than that seen in vegetative plants under the same conditions, though the increased responsiveness to UV did not diminish

the responses to RH, creating a complex interaction between RH and UV on the generative plants investigated in Experiment 2. In whole-plant morphology, exposure to UV radiation in 'Infinity Red' plants grown at 60 % RH had no effect on plant height, shoot length, the number of leaves per stem, internode length, leaf petiole lengths or bract petiole lengths, though it did result in a decrease in both plant diameter and the number of bracts per shoot compared to plants grown at 60 % RH and not exposed to UV. In plants grown at 90 % RH the effects of UV exposure were quite different, resulting in taller plants with longer shoots, a greater number of leaves per shoot and a greater number of bracts per shoot compared to plants grown at 90 % RH and not exposed to UV, though no effect was seen on internode length. Additionally, exposure to UV resulted in longer leaf and bract petioles and thereby a greater plant diameter than plants grown at 90 % RH and not exposed to UV. Responses to UV radiation in 'Bravo Bright Red' plants grown at 60 % RH differed to those of 'Infinity Red' plants. UV exposure in plants grown at 60 % RH had no effect on plant height, and while a decreased number of leaves per shoot and bracts per shoot resulted in longer internodes, the shoot length of these plants was decreased in comparison to plants not exposed to UV at 60 % RH. Additionally, despite there being no effect of UV exposure on leaf or bract petiole lengths, plants exposed to UV had a decreased diameter than plants not exposed to UV grown at 60 % RH. Again, the story for plants grown at 90 % RH differs, where plants exposed to UV had longer shoots and a greater number of both leaves and bracts per shoot, yet no effects were seen on internode length or plant height. Additionally, increased leaf and bract petiole lengths contributed to an increased plant diameter in comparison to plants not exposed to UV grown at 90 % RH.

From a whole-plant morphological perspective, the results described in response to UV radiation show limited agreement with previous findings. No reduction in plant height was seen in either of the cultivars with exposure to UV. The increased number of leaves and bracts per shoot in 'Bravo Bright Red' plants grown at 60 % RH and exposed to RH shows agreement with a previous study by Meijkamp et al. (2001), who found an increase in branching in response to UV exposure in *Vicia faba*, though the same study, together with Kakani et al. (2003), also found a reduction in internode length in response to enhanced UV radiation, a result that was not seen here in either of the cultivars in plants grown at either of the RH levels. That exposure to UV had opposing effects on plants grown at different RH levels, (e.g. plant diameter and the number of bracts per shoot in 'Infinity Red' plants, and plant diameter, shoot length and the number of both leaves and bracts per shoot in 'Bravo Bright Red' plants)

indicates a similar scenario to that found by Jansen and van den Noort (2000). They found that exposure to UV radiation caused either an opening or a closing of stomata, depending on the metabolic state of the guard cells. The findings described here may indicate an analogous scenario, where the magnitude and direction of several morphological responses are determined by the RH at which the plants are grown.

In addition to the responses seen as a result of UV exposure, general responses to differing levels of RH were seen in several parameters. In the 'Infinity Red' cultivar, plants grown at 90 % RH had an increased shoot length and increased internode length compared to plants grown at 60 % RH, though no effect was seen in plant height or the number of leaves and bracts per stem. Additionally, growth at 90 % RH resulted in a decrease in both leaf and bract petioles, though had no effect on plant diameter. In the 'Bravo Bright Red' cultivar, plants grown at 90 % RH showed and increases in both shoot length and the number of leaves per shoot, though no effect was seen on plant height or internode length, and the number of bracts per shoot was decreased in comparison to plants grown at 60 % RH. Additionally, a decrease in both leaf and bract petiole length contributed to a decreased plant diameter in plants grown at 90 % RH compared to those grown at 60 % RH. The results of Experiment 2 show agreement with the most general morphological response to high RH - an increase in shoot length – which is seen in both cultivars. A previous study on growth and morphological responses of poinsettia to increased RH found increases in plant height, plant diameter and internode length (Mortensen 2000). The results presented here agree with this singularly in the increase in internode length found in plants of the 'Infinity Red' cultivar grown at 90 % RH compared to those grown at 60 % RH. Diameter in 'Bravo Bright Red' plants was decreased with growth at 90 % RH compared to 60 % RH. This further illustrates intraspecific variation in poinsettia responses to environmental factors.

The intraspecific differences found between the responses of the two cultivars investigated come as no surprise as the two cultivars chosen for the generative growth chamber experiment were chosen due to their fundamental differences in growth and morphology. The two cultivars show general differences in size and growth vigour, traits which were hypothesised to result in differences in response to growth-modifying environmental factors. According to the North Carolina State University Department of Horticultural Science Poinsettia Trials, since its

introduction in 2008, optimal plants of the 'Infinity Red' cultivar have reached an average plant height of 16.1 inches (41 cm) with an average diameter of 13.4 inches (34 cm). They are also reported to show high growth vigour and be suitable for a market requiring larger bracts (North Carolina State University Department of Horticultural Science 2014b). 'Bravo Bright Red' plants on the other hand, while still reaching the impressive height of 14.9 inches (38 cm), and diameter of 12.1 inches (31 cm), show less growth vigour and their optimal size is smaller than that of 'Infinity Red' plants (North Carolina State University Department of Horticultural Science 2014a). Intraspecific differences in response to enhanced UV radiation have been reported for several species (Baroniya et al. 2011; Deckmyn & Impens 1999; Gehrke et al. 1996; Grammatikopoulos et al. 1998; Johanson et al. 1995; Kakani et al. 2003; Koti et al. 2007; Qaderi et al. 2008; Surabhi et al. 2009), which leads to the assumption that intraspecific differences in response to environmental factors may have a genetic basis.

The results of Experiment 3 indicate the response of 'Christmas Day' poinsettia plants to exposure to UV radiation as the sole changing environmental factor in a greenhouse experiment. From this we may get an idea of how UV radiation influences morphology, photosynthesis and anthocyanin content in poinsettia plants, though the intraspecific differences found in previous studies on several species serve as a reminder that the response of this cultivar to UV radiation may not provide a complete picture. The results presented in Experiment 3 tended to agree with the general responses to exposure to UV radiation. Plants exposed to UV had decreased plant height, shoot length and internode length compared to plants not exposed to UV, though neither the number of leaves nor the number of bracts were affected. In addition, though no effect was seen in the leaf petiole lengths, there was a reduction in plant diameter in plants exposed to UV compared to plants not exposed to UV. The reductions in plant size as a whole may be a result of a decreased shoot dry matter in plants exposed to UV compared to plants not exposed to UV.

Leaf morphology

The results presented here on leaf morphology and growth are, to an extent, in agreement with previous findings. The words 'to an extent' are used in this case as the above is true when looking at the effects of UV radiation in isolation, with the effects of RH notwithstanding. Reduced leaf area in leaves exposed to UV radiation was found in all three of the experiments,

regardless of the level of RH during growth. The competitive effect of UV with that of RH on leaf area in Experiments 1 and 2 is similar to previous findings in an investigation of plant responses to moderate and high RH (Fanourakis et al. 2011), where it was found that leaf expansion, as both leaf length and leaf area, was independent of the RH level experienced during growth. This was not entirely the case as both vegetative and generative leaf area showed a response to RH, yet the effect of UV on this parameter in particular was notably strong compared to the effect of UV on several other parameters. Plants exposed to UV radiation also showed a trend toward increased leaf thickness (lower SLA) in comparison to plants not exposed to UV radiation in all three of the experiments, though one exception was seen in the leaves of 90+UV 'Bravo Bright Red' plants, which were significantly thinner with exposure to UV radiation. This trend was overshadowed in vegetative plants (Experiment 1) by the significant effect of RH, which resulted in plants exposed to 90 % being significantly thinner (higher SLA) than plants exposed to 60 % RH, and while a similar trend was seen in response to RH in generative plants (Experiment 2), the effect was not overshadowed to the same extent as in vegetative plants. Interestingly, in a study on both evergreen and deciduous heathland shrub species, it has been found that leaf thickness in the evergreen species *Vaccinium vitis-idaea* increased in response to elevated UV radiation, while leaf thickness in two deciduous species, *Vaccinium myrtillus* and *Vaccinium uliginosum* is reduced under the same field conditions (Gehrke et al. 1996; Johanson et al. 1995), an indication of the variable nature of responses to UV radiation. The inhibition of leaf growth in response to UV radiation has been attributed to the inhibition of epidermal cell division (Nogués et al. 1998; Wargent et al. 2009), though it has been found that UV-B radiation enhanced epidermal cell expansion (Strid et al. 1994), resulting in leaves that were still significantly smaller in plants exposed to UV-B radiation, but leaf growth inhibition was greatly reduced due to the compensation of increased cell expansion as a counteraction to decreased cell division (Qaderi et al. 2008; Wargent et al. 2009). Conversely, Nogués et al. (1998) found an inhibition in epidermal cell expansion in response to exposure to UV-B radiation, while Mackerness et al. (1998) indicate destruction and a complete collapse of the upper epidermal cell layer. The epidermal cell layer plays a key role in both shoot and leaf expansion (Dale 1988; Savaldi-Goldstein et al. 2007; Wargent et al. 2009), meaning that effects of UV radiation on this layer will affect above-ground plant development, though the signalling pathways and mechanisms involved are numerous and convoluted.

The appearance of leaf bronzing as a response to UV radiation has previously been reported (Jansen & van den Noort 2000; Mackerness et al. 1998; Nedunchezhian & Kulandaivelu 1997). Leaf bronzing was seen in +UV leaves in both of the generative growth experiments (Experiments 2 and 3), while leaves in the vegetative growth phase showed no visible damage in response to UV radiation. Many studies report differences in response to elevated UV-B between species and cultivars, as well as between plants during different stages of growth (vegetative or reproductive) (Baroniya et al. 2011; Deckmyn & Impens 1998; Deckmyn & Impens 1999; Gehrke et al. 1996; Grammatikopoulos et al. 1998; Johanson et al. 1995; Kakani et al. 2003; Koti et al. 2007; Qaderi et al. 2008; Singh et al. 2012; Surabhi et al. 2009; Teramura et al. 1991). The lack of visible damage by UV radiation to vegetative plants agrees with previous findings by Deckmyn and Impens (1998), who found generative growth to be much more sensitive to UV-B radiation than vegetative growth in *Bromus catharticus* grown at three solar UV levels. Several reports state the importance of background PAR level in both the magnitude and direction of responses of plants to UV radiation (Cen & Bornman 1990; Lydon et al. 1986; Meijkamp et al. 2001; Wargent et al. 2009). Low level background PAR given in combination with UV radiation results in plants with an increased sensitivity to UV compared to that of plants exposed to high level background PAR given with UV radiation (Cen & Bornman 1990) and the ratio of UV-B/PAR is the factor determining whether UV radiation will be damaging or not (Deckmyn et al. 1994). Plants in all of the experiments performed in this study were given 150 µmol m^{-2} s^{-1} background PAR, a low dose in relation to the high doses given in previous experiments (e.g. 300 µmol m^{-2} s^{-1} in Liu et al. (1995), 700 µmol m^{-2} s^{-1}, 500 µmol m^{-2} s^{-1}, or 230 µmol m^{-2} s^{-1} in Cen & Bornman (1990)). This may be the reason for the leaf bronzing visible in plants exposed to UV radiation in Experiments 2 and 3. The absence of visible damage in vegetative plants may be a result of increased resistance to UV in vegetative plants as mentioned above, yet it may also be a result of the higher total daily light integral (DLI) received by the plants in Experiment 1. DLI is rate at which PAR reaches the plant canopy over the course of 24 h (Faust et al. 2005), and investigations into responses to DLI are often done in relation to responses of flowering (Oh et al. 2009; Pramuk & Runkle 2005a; Pramuk & Runkle 2005b). In this instance, however, it is postulated that the higher DLI received by vegetative plants compared to generative plants resulted in an increase in plant resistance to UV radiation, and that the UV-B/PAR ratio over time (e.g. per day) affects plant resistance to UV-induced damage. Furthermore, that the UV radiation was given in the middle of the dark period in vegetative plants and at the end of the light period in generative plants

may have played a role in the differences in sensitivity to UV seen between vegetative and generative plants, though further investigation is needed in order to confirm this.

The results presented in Experiment 1 show the strong effects of RH on vegetative Poinsettia morphology. The differences found between +UV and -UV treatments were substantially smaller than the differences found between the two levels of RH. The same cannot be said for generative plants, as the results of Experiment 2 indicate a complex interaction between RH and UV radiation on the morphological traits of the plants investigated. The fact that some parameters show a stronger response to RH, while others show a stronger response to UV radiation, as well as the fact that these parameters differ intraspecifically, indicates a need to investigate more thoroughly the mechanisms controlling each trait in the context of the environmental factors investigated here in order to better understand the driving force of the morphological differences.

The role of phytohormones such as the auxin indole-3-acetic acid (IAA) and gibberellins (GAs) in plant morphology are well known, with IAA associated with apical dominance and the promotion of cell growth (Lambers et al. 2008; Taiz & Zeiger 2010) and GAs being best known for their role in cell division and elongation, and strong stimulation of stem elongation (Lambers et al. 2008; Taiz & Zeiger 2010). The destruction of IAA has been reported in rice leaves (*Oryza sativa*) as a result of the stimulation of peroxidase and IAA oxidase in response to UV exposure (Huang et al. 1997). Additionally, downregulation of auxin-responsive genes in UV-acclimated plants, and impacts on genes regulating auxin distribution in plants exposed to acute UV doses, was reported in *Arabidopsis thaliana* (Hectors et al. 2007), along with a decrease in the amount of free auxins present in young leaf tissues which accompanied a decrease in leaf area in response to UV exposure (Hectors et al. 2012). Regarding the response of gibberellins to UV radiation, an increase in transcript abundance of a GA2-oxidase (*GA2ox1*), which hydroxilates GA to an inactive form, coupled with inhibition of transcript accumulation of a GA biosynthesis gene was found in *Arabidopsis thaliana* (Hayes et al. 2014), as well as differential expression of gibberellin metabolic genes in response to low doses of UV radiation (Hectors et al. 2007). Additionally, application of an inhibitor of gibberellin biosynthesis, Paclobutrazol, resulted in enhanced tolerance of UV radiation in soybean (*Glycine max*) through the induction of a thicker epicuticular wax layer and thickening of the

leaves (Kraus et al. 1995). Plant hormone responses to relative air humidity are little-investigated, though a study by Lee et al. (1972) indicated no response of either auxin or gibberellin to high RH (90 %) compared to low (50 %) RH. The results of the abovementioned studies indicate the potential role of auxin (Meijkamp et al. 2001) and gibberellin in transduction pathways leading to photomorphogenic responses to UV radiation.

Stomatal responses to air humidity and UV radiation

The response of stomata to growth at high RH has been well documented in several species, in intact plants (Aasamaa & Sober 2011; Rezaei Nejad & Van Meeteren 2005; Rezaei Nejad & van Meeteren 2007; Rezaei Nejad & van Meeteren 2008), rooted cuttings (Fanourakis et al. 2011; Fordham et al. 2001; Torre et al. 2003) and micropropagated plants (Santamaria et al. 1993). Exposure to a low vapour pressure deficit (VPD), corresponding to a threshold value of RH > 85 % (Torre & Fjeld 2001), results in malfunctioning stomata across the board, which fail to respond to stimuli signalling stomatal closure such as darkness, desiccation and exogenous ABA application. In *Corylus maxima*, both rooted cuttings and intact plants displayed the same reduced stomatal response to darkness, desiccation or ABA treatment as closing stimuli (Fordham et al. 2001). Leaves of micropropagated *Delphinium* plants produced *in vitro* showed similar limitations in stomatal control, with larger and more frequent stomata responding only to a limited degree to closing stimuli (Santamaria et al. 1993). In this instance, stomata were especially non-responsive to ABA, a result that the authors attributed to the high cytokinin concentration in the growth medium (Santamaria et al. 1993), as cytokinins induce partial stomatal opening (Wright & Murphy 1982). Leaves were found to have a lower endogenous ABA concentration when grown at high RH for both *Tradescantia virginiana* (Rezaei Nejad & van Meeteren 2007) and *Rosa hybrida* (Arve et al. 2013; Fanourakis et al. 2011), most likely a result of a lower transpiration rate under high RH conditions. Leaf ABA concentration is both influenced by root ABA transport via the xylem (Fanourakis et al. 2011) and by the balance between biosynthesis and degradation of ABA produced in the leaves (Arve et al. 2013). Rose leaves grown at high RH have been shown to not increase their ABA level during the dark period, resulting in a lack of closure signal for the stomata (Arve et al. 2013). This lack of increase in ABA during the dark period has been proposed to be a result of the lowered transpiration rate in plants grown a high RH. The lowered transpiration rate in leaves grown at high RH may contribute to a decrease in nutrient uptake, and therefore stomata may need to remain open in order to maximise nutrient uptake (Arve & Torre 2015). Low ABA

concentration in the leaves during growth has therefore been proposed to contribute to the development of malfunctioning stomata (Arve et al. 2013). The production of malfunctioning stomata results in plants with leaves that are unable to maintain an adequate water status when transferred to lower RH, which may have lethal consequences for the plant. Malfunctioning stomata are furthermore detrimental in the plant production industry, where post-harvest keeping quality is of high importance (Mortensen & Gislerød 1999; Mortensen 2000; Torre & Fjeld 2001).

Several authors have reported stomatal closure and reduced conductance in response to UV radiation (He et al. 2005; Jansen & van den Noort 2000; Negash & Björn 1986; Nogués et al. 1999; Tossi et al. 2009; Tossi et al. 2014) while Eisinger et al. (2000) found that UV-B works to open stomata and that the action spectrum for stomatal opening has a peak at 280 nm. Such a broad spectrum of reported results allows for the conclusion that plant responses to UV radiation are highly complex and sensitive to differences in any of the many factors which make up growth conditions. Stomatal responses to UV radiation are wavelength-dependent (Negash & Björn 1986), with differing effects observed in response to UV-A, UV-B and UV-C radiation. UV-A radiation works in conjunction with blue light to open stomata (Eisinger et al. 2000; Eisinger et al. 2003), corresponding to those wavelengths that drive photoreactivation (Jansen et al. 1998), while UV-C radiation stimulates stomatal closure (Murali & Saxe 1984; Wright & Murphy 1982). Stomatal control by UV-B radiation is slightly more controversial, with studies reporting both stomatal opening and closure in response to UV-B radiation (Eisinger et al. 2000; Eisinger et al. 2003; He et al. 2005; Jansen & van den Noort 2000; Tossi et al. 2014), with differing results according to UV-B fluence rate, duration and wavelength (Jenkins 2009; Tossi et al. 2014), additional PAR fluence rate (Jansen & van den Noort 2000; Negash & Björn 1986; Nogués et al. 1999), additional environmental factors (Jenkins 2009) and guard cell metabolic state (Jansen & van den Noort 2000). Stomatal opening as a response to low fluence rates of UV-B radiation has been found in *Arabidopsis thaliana* (Eisinger et al. 2000; Eisinger et al. 2003), and Jansen & van den Noort (2000) found that higher fluence rates of UV-B induce stomatal closure when given in combination with low PAR fluence rates, yet when given with high PAR fluence rates induced stomatal opening. However, the closure of stomata in response to UV-B radiation is by far the most common response found (He et al. 2005; Negash & Björn 1986; Nogués et al. 1999). This study aimed to test the capacity of UV

radiation as a stomatal closing signal to ameliorate the detrimental effects of RH on stomatal functioning in two cultivars of generative poinsettia grown in controlled growth chambers.

The results presented in Experiment 2 show stomatal responses of two poinsettia cultivars, 'Infinity Red' and 'Bravo Bright Red' in the generative phase of growth, grown under one of two levels of RH (60 % or 90 %) and either exposed (+UV) or not exposed (-UV) to UV radiation. Stomatal imprints and conductance measurements were taken both near the end of the light period and one hour after the start of the dark period in order to ascertain stomatal function in response to a closing stimulus (darkness). A comparison of the measurements of stomatal aperture size and leaf stomatal conductance rates between light and dark conditions indicated malfunctioning stomata, seen as the reduced ability of plants to close their stomata when exposed to a closing stimulus, in both cultivars grown at 90 % RH regardless of whether or not the plants received UV radiation. These results are in agreement with previous findings on stomatal responses to high RH.

Growth of plants at 90 % RH resulted in an increase in bract conductance during the dark period compared to the light period, though only in plants not exposed to UV. It was originally thought that this was an anomalous result, however, all ten replications had equally high conductance. It may be that this is the normal response of conductance in bract stomata and that exposure to UV altered this. Should this be the case then it may be said that exposure to UV radiation at 90 % RH in 'Infinity Red' bracts results in the closure of stomata in darkness, or the ability of stomata to respond to a closing stimulus. This is mere speculation and further investigation would need to be undertaken to further our understanding of the processes taking place here. The response was not reflected in measurements of stomatal aperture, though it must be noted that stomatal aperture imprints were taken inside the growth chambers while conductance measurements were taken outside the chamber in air with 40-50 % RH, making comparisons between aperture measurements and conductance measurements uncertain. Leaves of the plants grown at 90 % RH and measured in darkness show a reduction in stomatal conductance in response to exposure to UV compared to plants not exposed to UV. This difference was not reflected in stomatal aperture size measurements. Leaves and bracts grown at 60 % RH and measured in darkness show a similar trend, where conductance is lowered in leaves and bracts exposed to UV compared to those not exposed to UV, though this difference is very slight, and

in leaves is not reflected in stomatal aperture size measurements. Again, stomatal imprints were taken inside the growth chambers while conductance measurements were taken outside in air with 40-50 % RH, making comparisons between aperture measurements and conductance measurements uncertain. A slightly different scenario is seen in 'Bravo Bright Red' plants, where exposure to UV radiation under light conditions resulted in an increase in leaf conductance compared to plants grown at 90 % RH with no UV exposure, yet in plants grown at 60 % RH the effect of UV exposure was the opposite. These effects are reflected in bract conductance measured in the light and leaf conductance measured in the dark, though in bract conductance measured in the dark no effects of UV were seen.

The light response curves presented in Experiment 3 show the response in photosynthesis, transpiration rate and stomatal conductance to increasing light intensities from completely dark to saturating intensity (600 µmol m^{-2} s^{-1}) in plants exposed or not exposed to UV radiation. RH was not a factor in this experiment, being maintained at 70 %, therefore these results indicate solely the plant photosynthetic and stomatal responses to UV exposure compared to plants not exposed to UV. While the response of photosynthesis showed no differences between +UV and –UV plants (discussed in more detail later), both transpiration rate and stomatal conductance are higher in +UV plants than –UV plants at all light intensities. Though stomatal aperture was not measured in Experiment 3, the light response curves indicate a greater stomatal aperture during the light period in plants exposed to UV radiation during growth. Notably, both transpiration rate and stomatal conductance rate show a slight increase during exposure to darkness compared to the lowest light level given (approx. 25 µmol m^{-2} s^{-1}), indicating a malfunction in stomatal function in response to darkness and increased irradiance. A previous study on buckwheat (*Fagopyrum esculentum*) has shown that UV radiation can affect transpiration and thereby reduce water use efficiency (Gaberščik et al. 2002).

ABA plays an intrinsic role in the control of stomatal movement and the concentration of ABA in plant tissues increases or decreases in response to environmental signals (Arve et al. 2013). Endogenous ABA levels are decreased in plants grown at continuously high RH (> 85 %) compared to plants grown at lower RH levels (Fanourakis et al. 2011; Rezaei Nejad & van Meeteren 2007), a result found to be due to the decrease in activity levels of β-glucosidase, an enzyme which converts the storage form of ABA (ABA-GE) to active ABA, in plants grown

at high RH (Arve et al. 2013). Conversely, UV radiation has been shown to increase ABA concentration in maize (*Zea mays*) (Tossi et al. 2009). The closure of stomata induced by UV radiation requires NO and H_2O_2 generation (He et al. 2005; Tossi et al. 2014), a process which is mediated by UV radiation-induced ABA and plant NADPH oxidase (pNOX) (Tossi et al. 2009). The aim of this study was to combat the reduction of ABA concentration in plants grown at 90 % RH through exposure to UV radiation (see Figure 10). Figure 10 illustrates the ABA pathway induced by UV radiation as described in Figure 1 by Tossi et al. (2014), in addition to the findings of Arve et al. (2013) that growth at high (> 85 %) results in lower ABA concentration in plant tissues. The aim of this study was to combat the ABA reduction induced by growth at high RH (red line) with the ABA increase induced by UV radiation (blue arrow). However, the results indicate that, in the case of UV combined with RH (Experiment 2), the stomata of plants responded more strongly to RH, as growth at high RH resulted in malfunctioning stomata regardless of UV exposure. Additionally, Experiment 3 indicated higher transpiration and conductance in plants exposed to UV, which indicates stomatal opening in plants exposed to UV radiation. Though this would agree with the findings of Eisinger et al. (2000), it was unexpected and indicates disagreement with the pathway proposed by Tossi et al. (2014).

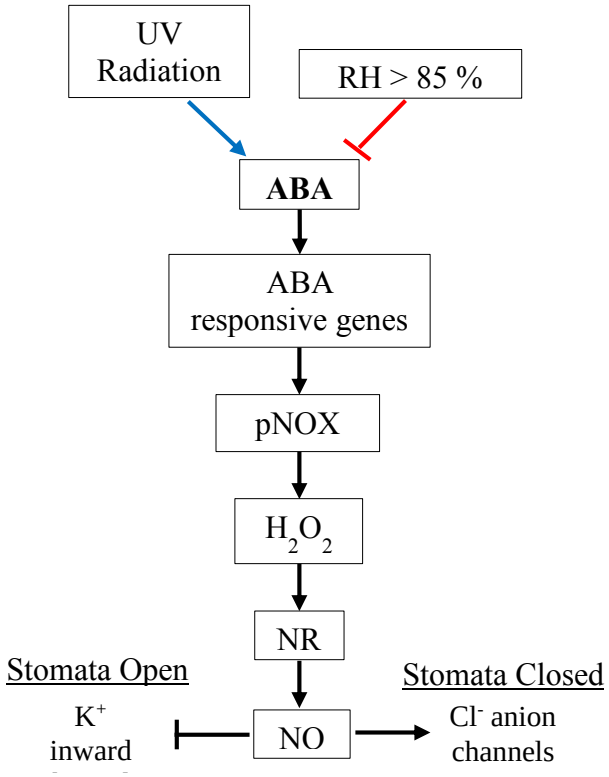


Figure 10. Schematic illustration of the signalling cascade induced by ABA in leaf tissue, as well as ABA regulation by UV-B and high RH (RH > 85 %), to induce stomatal closure. Arrows indicate induction, black bars indicate inhibition. This study wished to investigate whether induction of ABA by UV Radiation (blue arrow) may be stronger than inhibition by growth at RH > 85 % (red line). Adapted from original figure in Tossi et al. (2014).

Photosynthetic responses to UV radiation

Numerous studies have shown damaging effects of UV-B radiation on the photosynthetic apparatus (Friso et al. 1995; Jansen et al. 1996; Strid et al. 1994; Teramura & Sullivan 1994) in both direct and indirect ways. Photosystem II has been shown to be the main target of UV-B-induced damage, as UV-B radiation has a strong effect on the turnover rates of the D1 polypeptide (Teramura & Sullivan 1994). In an environmentally relevant level of background PAR, low fluences of UV-B have also been shown to increase the turnover rate of the D2 protein, resulting in further decreased stability of Photosystem II (Jansen et al. 1996). The formation of photoproducts such as pyrimidine dimers results in damage to DNA molecules (Strid et al. 1994). The light-requiring repair enzyme, photolyase, is responsible for the splitting of cyclobutane pyramidine dimers in a process called photoreactivation, which is driven by both blue light and UV-A radiation (Strid et al. 1994; Teramura & Sullivan 1994). Further decreases in photosynthetic capacity in response to UV-B radiation may result from the build-up of reactive oxygen species (ROS) due to interactions between UV-B and molecular oxygen (Strid et al. 1994). ROS further increase the instability of Photosystem II and require detoxification by antioxidants to prevent damage (Strid et al. 1994). Indirectly, photosynthesis may be affected by several UV-B- induced responses including increases in epidermal cell size, increases in leaf thickness (Johanson et al. 1995), changes in epicuticular wax, effects on stomatal function, accumulation of UV-B- absorbing compounds in the vacuoles of the epidermis and changes in plant canopy morphology (Strid et al. 1994; Teramura & Sullivan 1994). These factors work separately or in combination to increase the path length of UV-B into the leaf in order to attenuate the potentially damaging effects. However, increasing the path length for UV-B also increases the path length for visible light needed for photosynthesis, indirectly resulting in a decrease in photosynthetic capacity. The results presented here show neither an effect of UV radiation nor RH on photosynthesis during growth for either of the cultivars investigated in Experiment 2. The purpose of the light response curves generated in Experiment 3 was to analyse potential reductions in photosynthetic capacity that are not apparent in single measurements. No differences whatsoever were found between –UV and +UV plants at any of the light intensities, allowing for the conclusion that UV exposure had no influence on the photosynthetic capacity of the plants investigated here. There is, however, still the possibility that the UV-B radiation emitted from the fluorescent tubes did result in the production of pyrimidine dimers, but that UV-A radiation from the lamps or the natural background light initiated photolyase-mediated photoreactivation, though there is no way of knowing this for certain without further investigation.

Chlorophyll and anthocyanin content in response to air humidity and UV radiation

There have been few reports on the effects of RH on chlorophyll content, though one study on micropropagated *Doritaenopsis* reported an increase in the chlorophyll content of the plants with increasing relative air humidity (Jeon et al. 2006). The response of chlorophyll content to UV radiation has been shown to be varied, and though the majority of experiments report a decrease in plant chlorophyll content (Bornman & Vogelmann 1991; Cen & Bornman 1990; Frohnmeyer & Staiger 2003; Jansen et al. 1998; Lingakumar et al. 1999; Mahdavian et al. 2008; Qaderi et al. 2008; Strid et al. 1994; Surabhi et al. 2009) in response to UV exposure, instances of only slight or no effect on chlorophyll content (Barsig & Malz 2000; Grammatikopoulos et al. 1998; Liu et al. 1995), as well as increases in chlorophyll content (Deckmyn & Impens 1998; Deckmyn & Impens 1999) have been reported. Chlorophyll is a chlorin derivative with a central Mg atom which plays a pivotal role in both light harvesting and light conversion in photosynthesis (Zvezdanović et al. 2009). In an experiment involving both *in vitro* and *in situ* investigation of the effects of UV-A, UV-B and UV-C on chlorophyll found that UV radiation causes irreversible chlorophyll bleaching, and that the mechanisms of damage induced by UV-A and UV-B on chlorophyll may differ to those induced by UV-C (Zvezdanović et al. 2009). Additionally, the rate of bleaching depends on the UV-photon energy input as well as the molecular organisation of chlorophylls in the thylakoid (Zvezdanović et al. 2009). The aim of this experiment was to provide UV radiation at a low enough dose that damage would not occur, but high enough that the UV radiation would act as a signal for plant morphogenesis. The results presented in Experiment 2 indicate that leaf chlorophyll content was influenced by both RH and UV radiation and that the effects of UV radiation agree with those reported by Deckmyn and Impens (1998) and Deckmyn and Impens (1999) in that exposure to UV radiation resulted in an increase in leaf chlorophyll content in comparison to plants not exposed to UV. This may be a result of increased leaf thickness in response to UV radiation, where chlorophyll concentration per unit leaf area is increased. The effect of RH resulted in a reduction in leaf chlorophyll content in –UV plants grown at 90 % RH compared to all the other treatments, which does not agree with the findings of Jeon et al. (2006), though further investigation into the responses of chlorophyll to relative air humidity is needed.

Anthocyanins collect in the vacuoles of epidermal cells in many plant species and serve often as a protective mechanism in response to UV radiation (Strid et al. 1994). The accumulation of

flavonoids is a well-documented response to UV radiation (Guo et al. 2008; Hollosy 2002; Mahdavian et al. 2008; Mpoloka 2008) as flavonoids such as anthocyanins provide protection for DNA against UV-induced damage by attenuating the amount of UV radiation reaching the photosynthetic apparatus (Mahdavian et al. 2008; Stapleton & Walbot 1994). UV radiation causes an increase in anthocyanin concentration through upregulation of biosynthetic genes and causes changes in their concentration profile through modifications in the transcript levels of catalysing enzymes (Guo et al. 2008; Martinez-Luscher et al. 2014). In poinsettia production, the accumulation of anthocyanins in bracts directly influences the marketability of the plants (Slatnar et al. 2013). Poinsettia bract development is characterised by morphogenesis as well as colorimetric alteration, with a decrease in chlorophyll content and an accumulation of anthocyanins occurring with bract development (Slatnar et al. 2013). Bract morphology and anthocyanin content were investigated due to the high importance of poinsettia bracts in commercial production. In Experiment 2, where plants were in the generative growth phase and exposed to both UV radiation and two levels of RH, the bracts on both 'Infinity Red' plants and 'Bravo Bright Red' plants showed the same trends. Plants of both cultivars showed a significant effect of UV, yet the interaction between RH and UV resulted in the magnitude and direction of the UV effect being determined by the level of air humidity at which the plants were grown. That is, in plants grown at 90 % RH exposure to UV resulted in more bracts per shoot compared to plants grown at 90 % RH and not exposed to UV, yet the opposite trend was seen in plants grown at 60 % RH, where exposure to UV resulted in a decrease in the number of bracts per shoot. Similar effects are seen in bract petiole length, though the effect of UV was not significant at 60 % RH, and in bract area, though bract thickness showed a decrease with exposure to UV radiation at both levels of air humidity. Both cultivars also showed effects of RH, which in 'Infinity Red' plants resulted in a reduction in petiole length and bract area, as well as an increase in bract thickness in plants grown at 90 % RH compared to plants grown at 60 % RH, while no effect was seen on the number of bracts. In 'Bravo Bright Red' plants, plants grown at 90 % RH showed a reduction in the number of bracts per shoot, bract petiole length and bract area compared to plants grown at 60 % RH, and an increase in bract thickness relative to plants grown at 60 % RH and exposed to the same light environment (i.e. the increase in thickness was seen in bracts grown at 90 % RH and exposed to UV compared to bracts grown at 60 % RH and exposed to UV, but not those not exposed to UV). In Experiment 3, where UV radiation was the sole changing environmental parameter, bracts on +UV plants were found to be significantly smaller, thicker and have a higher anthocyanin content than bracts on –UV plants, though there was no significant difference in the number of bracts

between +UV and –UV plants. These results show agreement with previous findings of an increase in anthocyanin content with exposure to UV. Further investigation into the anthocyanin content in bracts exposed to different levels of air humidity during growth in combination with exposure to UV would help shed light on the combined effects of these two environmental parameters on poinsettia bract colouration. As mentioned above, two of the responses to UV radiation are the decrease in leaf area and increase in the size of leaf epidermal cells, thereby increasing the thickness of the leaf. It is likely that the decrease in bract size and the increased bract thickness found in +UV bracts in Experiment 3 is analogous to the responses generally found in leaves.

Implications for commercial production

The results presented on 'Christmas Day' poinsettia (Experiment 3) performed in a greenhouse provide a general indication of the morphological, stomatal, photosynthetic and chemical responses of poinsettia to UV radiation. It has been shown here that UV radiation may contribute to making poinsettia more compact in height and diameter, though the dose used here was probably too high as it resulted in leaf bronzing. It is possible that a lower UV dose combined with PAR of a greater intensity may reduce the visible damage to the plants, making the use of UV more viable as an option for commercial production, though further study would need to be done. The results from Experiments 1 and 2 indicate the responses of poinsettia to a combination of RH and UV radiation, at the same time highlighting that both the ontogenetic stage of the plant, as well as the plant cultivar play a role in determining responses to environmental parameters. UV radiation, when given in combination with 90 % RH in vegetative plants had little effect as the plants responded more strongly to the RH effect. This was not true in generative plants, where some parameters responded more strongly to RH and others to UV, resulting in no clear pattern. Visible cyathia were delayed by a day in both 'Infinity Red' and 'Bravo Bright Red' plants grown at 90 % RH, though exposure to UV radiation at this RH level ameliorated this. Flowering has previously been shown to be accelerated by UV-C radiation in *Arabidopsis thaliana* (Martinez et al. 2004) through a stress-activated increase in salicylic acid. Experiment 3 was performed in a greenhouse compartment in the season when poinsettia is commonly grown (September-December). Thus, from this experiment it is possible to discuss implications for commercial production. Plant height was reduced by 16 % compared to control and is in the same range as temperature drop treatments (Moe et al. 1992b). Increasing the amount of blue light (Britz & Sager 1990; Brown et al. 1995;

Mortensen & Fjeld 1998), increasing the red (R)/far red (FR) light ratio through the use of FR-screening filters (Rajapakse & Kelly 1992; Rajapakse et al. 1999) and exposing plants to a negative DIF (day temperature < night temperature) (Berghage & Heins 1991; Moe & Heins 1990) have also been shown to be effective means of controlling plant height, though the control of plant height by negative DIF in poinsettia also resulted in a delay in flowering (visible cyathia) (Moe et al. 1992a). Reports of the abovementioned treatments indicate an average plant height reduction of 25 %, which is more effective than that seen here. Furthermore, the combination of temperature drop and UV radiation resulted in a 30 % more effective reduction in plant height than temperature drop alone in pea plants (Roro 2015). The control of plant size in greenhouses is important for several reasons, including increasing the number of plants per area in the greenhouse to produce the maximum number of plants and increase profits, keeping in line with consumer demands and creating more robust plants that are easier to package and transport. The less effective height control of UV compared to other methods in combination with the potential damage to plants through UV exposure leads to the conclusion that there are safer, more effective ways of controlling plant height in commercial production. However, investigations should be made into ameliorating the damaging effects of UV through increasing background PAR intensity or using screened UV light sources, and finding the correct combination of UV and other environmental conditions, especially when taking into account the potential role of UV radiation in crop disease control and promotion of flowering time.

Conclusions

The hypothesis that the use of UV radiation may help counter the negative effects of high RH in the commercial production of Poinsettia has been refuted. The combination of high RH and UV radiation resulted in tall plants with smaller leaves and longer petioles in the case of ‘Infinity Red’ and average height plants with larger leaves, but fewer, larger bracts in the case of ‘Bravo Bright Red’ plants. Unfortunately, such traits are undesirable in commercial Poinsettia production, where more compact, robust plants are required. The effects of UV under moderate air humidity in a greenhouse showed promising results, with shorter plants and increased anthocyanin content in bracts, though the dose was too high and the leaves were damaged. Further investigation in these conditions may provide positive results, especially in combination with differing environmental conditions.

References

Aasamaa, K. & Sober, A. (2011). Responses of stomatal conductance to simultaneous changes in two environmental factors. *Tree Physiology*, 31: 855-864.

Arve, L. E., Terfa, M. T., Gislerod, H. R., Olsen, J. E. & Torre, S. (2013). High relative air humidity and continuous light reduce stomata functionality by affecting the ABA regulation in rose leaves. *Plant, Cell & Environment*, 36 (2): 382-92.

Arve, L. E. & Torre, S. (2015). *Discussion of results* (07-05-2015).

Bævre, O., Fjeld, T. & Moe, R. (1994). Poinsettia production in the north. In Strømme, E. (ed.) *The Scientific Basis of Poinsettia Production*. Ås, Norway: Agricultural University of Norway.

Ballare, C. L., Scopel, A. L., Stapleton, A. E. & Yanovsky, M. J. (1996). Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insects in *Datura ferox*. *Plant Physiology*, 112 (1): 161-170.

Baroniya, S. S., Kataria, S., Pandey, G. P. & Guruprasad, K. N. (2011). Intraspecific variation in sensitivity to ambient ultraviolet-B radiation in growth and yield characteristics of eight soybean cultivars grown under field conditions. *Brazilian Journal of Plant Physiology*, 23: 197-202.

Barsig, M. & Malz, R. (2000). Fine structure, carbohydrates and photosynthetic pigments of sugar maize leaves under UV-B radiation. *Environmental and Experimental Botany*, 43 (2): 121-130.

Berghage, R. D. & Heins, R. D. (1991). Quantification of temperature effects on stem elongation in poinsettia. *HortScience*, 116 (1): 14-18.

Bornman, J. F. & Vogelmann, T. C. (1991). Effect of UV-B radiation on leaf optical properties measured with fibre optics. *Journal of Experimental Botany*, 42 (4): 547-554.

Britz, S. J. & Sager, J. C. (1990). Photomorphogenesis and photoassimilation in soybean and sorghum grown under broad spectrum or blue-deficient light sources. *Plant Physiology*, 94 (2): 448-454.

Brown, B. A. & Jenkins, G. I. (2008). UV-B signaling pathways with different fluence-rate response profiles are distinguished in mature *Arabidopsis* leaf tissue by requirement for UVR8, HY5, and HYH. *Plant Physiology*, 146 (2): 576-588.

Brown, C. S., Schuerger, A. C. & Sager, J. C. (1995). Growth and photomorphogenesis of pepper plants under red light-emitting diodes with supplemental blue or far-red lighting. *HortScience*, 120 (5): 808-813.

Caldwell, M. M., Teramura, A. H., Tevini, M., Bornman, J. F., Björn, L. O. & Kulandaivelu, G. (1995). Effects of increased solar ultraviolet radiation on terrestrial plants. *Ambio*, 24 (3): 166-173.

Cen, Y.-P. & Bornman, J. F. (1990). The response of bean plants to UV-B radiation under different irradiances of background visible light. *Journal of Experimental Botany*, 41 (11): 1489-1495.

Cloix, C., Kaiserli, E., Heilmann, M., Baxter, K. J., Brown, B. A., O'Hara, A., Smith, B. O., Christie, J. M. & Jenkins, G. I. (2012). C-terminal region of the UV-B photoreceptor UVR8 initiates signaling through interaction with the COP1 protein. *PNAS*, 109 (40): 16366-70.

Dale, J. E. (1988). The control of leaf expansion. *Annual Review of Plant Physiology and Plant Molecular Biology*, 39 (1): 267-295.

Deckmyn, G., Martens, C. & Impens, I. (1994). The importance of the ratio UV-B/photosynthetic active radiation (PAR) during leaf development as determining factor of plant sensitivity to increased UV-B irradiance: effects on growth, gas exchange and pigmentation of bean plants (*Phaseolus vulgaris* cv. Label). *Plant, Cell & Environment*, 17 (3): 295-301.

Deckmyn, G. & Impens, I. (1998). Effects of solar UV-B irradiation on vegetative and generative growth of Bromus catharticus. *Environmental and Experimental Botany*, 40 (2): 179-185.

Deckmyn, G. & Impens, I. (1999). Seasonal responses of six *Poaceae* to differential levels of solar UV-B radiation. *Environmental and Experimental Botany*, 41 (2): 177-184.

Demkura, P. V. & Ballare, C. L. (2012). UVR8 mediates UV-B-induced *Arabidopsis* defense responses against Botrytis cinerea by controlling sinapate accumulation. *Molecular Plant*, 5 (3): 642-52.

Eisinger, W., Swartz, T. E., Bogomolni, R. A. & Taiz, L. (2000). The ultraviolet action spectrum for stomatal opening in broad bean. *Plant Physiology*, 122 (1): 99-106.

Eisinger, W. R., Bogomolni, R. A. & Taiz, L. (2003). Interactions between a blue-green reversible photoreceptor and a separate UV-B receptor in stomatal guard cells. *American Journal of Botany*, 90 (11): 1560-6.

Fanourakis, D., Carvalho, S. M. P., Almeida, D. P. F. & Heuvelink, E. (2011). Avoiding high relative air humidity during critical stages of leaf ontogeny is decisive for stomatal functioning. *Physiologia Plantarum*, 142 (3): 274-286.

Faust, J. E., Holcombe, V., Rajapakse, N. C. & Layne, D. R. (2005). The effect of daily light integral on bedding plant growth and flowering. *HortScience*, 40 (3): 645-649.

Fordham, M. C., Harrison-Murray, R. S., Knight, L. & Evered, C. E. (2001). Effects of leaf wetting and high humidity on stomatal function in leafy cuttings and intact plants of *Corylus maxima*. *Physiologia Plantarum*, 113 (2): 233-240.

Francois, L. E., Donovan, T. J. & Maas, E. V. (1991). Calcium deficiency of artichoke buds in relation to salinity. *HortScience*, 26 (5): 549-553.

Friso, G., Vass, I., Spetea, C., Barber, J. & Barbato, R. (1995). UV-B-induced degradation of the D1 protein in isolated reaction centres of photosystem II. *Biochimica et Biophysica Acta (BBA) - Bioenergetics*, 1231 (1): 41-46.

Frohnmeyer, H. & Staiger, D. (2003). Ultraviolet-B radiation-mediated responses in plants. Balancing damage and protection. *Plant Physiology*, 133 (4): 1420-1428.

Gaberščik, A., Vončina, M., Trošt, T., Germ, M. & Björn, L. O. (2002). Growth and production of buckwheat (*Fagopyrum esculentum*) treated with reduced, ambient and enhanced UV-B radiation. *Journal of Photochemistry and Photobiology B: Biology*, 66: 30-36.

Gehrke, C., Johanson, U., Gwynn-Jones, D., Björn, L. O., Callaghan, T. V. & Lee, J. A. (1996). Effects of enhanced ultraviolet-B radiation on terrestrial subarctic ecosystems and implications for interactions with increased atmospheric CO2. *Ecological Bulletins*, 45: 192-203.

Gislerød, H. R. (1999). *The role of calcium on several aspects of plant and flower quality from a floricultural perspective*. International Symposium on Growng Media and Hydorponics: Acta Horticulturae. 345-352 pp.

Grammatikopoulos, G., Kyparissis, A., Drilias, P., Petropoulou, Y. & Manetas, Y. (1998). Effects of UV-B radiation on cuticle thickness and nutritional value of leaves in two mediterranean evergreen sclerophylls. *Journal of Plant Physiology*, 153 (3–4): 506-512.

Grange, R. I. & Hand, D. W. (1987). A review of the effects of atmospheric humidity on the growth of horticultural crops. *The Journal of Horticultural Science and Biotechology*, 62 (2): 125-134.

Guo, J., Han, W. & Wang, M.-H. (2008). Ultraviolet and environmental stresses involved in the induction and and regulation of anthocyanin biosynthesis: A review. *African Journal of Biotechnology*, 7 (25): 4966-4972.

Hayes, S., Velanis, C. N., Jenkins, G. I. & Franklin, K. A. (2014). UV-B detected by the UVR8 photoreceptor antagonizes auxin signaling and plant shade avoidance. *PNAS*, 111 (32): 11894-11899.

He, J., Xu, H., She, X., Song, X. & Zhao, W. (2005). The role and the interrelationship of hydrogen peroxide and nitric oxide in the UV-B-induced stomatal closure in broad bean. *Functional Plant Biology*, 32 (3): 237-247.

Hectors, K., Prinsen, E., De Coen, W., Jansen, M. A. K. & Guisez, Y. (2007). *Arabidopsis thaliana* plants acclimated to low dose rates of ultraviolet B radiation show specific changes in morphology and gene expression in the absence of stress symptoms. *New Phytologist*, 175 (2): 255-270.

Hectors, K., van Oevelen, S., Guisez, Y., Prinsen, E. & Jansen, M. A. K. (2012). The phytohormone auxin is a component of the regulatory system that controls UV-mediated accumulation of flavonoids and UV-induced morphogenesis. *Physiologia Plantarum*, 145 (4): 594-603.

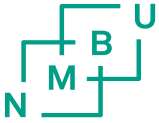
Hoffman, G. J., Rawlins, S. L., Garber, M. J. & Cullen, E. M. (1971). Water relations and growth of cotton as influenced by salinity and relative humidity. *Agronomy Journal*, 63 (6): 822-826.
Hollosy, F. (2002). Effects of ultraviolet radiation on plant cells. *Micron*, 33 (2): 179-97.
Hovenden, M. J., Vander Schoor, J. K. & Osanai, Y. (2012). Relative humidity has dramatic impacts on leaf morphology but little effect on stomatal index or density in *Nothofagus cunninghamii* (Nothofagaceae). *Australian Journal of Botany*, 60 (8): 700-706.
Huang, S., Dai, Q., Peng, S., Chavez, A. Q., Miranda, M. L. L., Visperas, R. M. & Vergara, B. S. (1997). Influence of supplemental ultraviolet-B on indoleacetic acid and calmodulin in the leaves of rice (*Oryza sativa* L.). *Plant Growth Regulation*, 21 (1): 59-64.
Jansen, M. A. K., Gaba, V., Greenberg, B. M., Mattoo, A. K. & Edelman, M. (1996). Low threshold levels of ultraviolet-B in a background of photosynthetically active radiation trigger rapid degradation of the D2 protein of photosystem-II. *The Plant Journal*, 9 (5): 693-699.
Jansen, M. A. K., Gaba, V. & Greenberg, B. M. (1998). Higher plants and UV-B radiation: Balancing damage, repair and acclimation. *Trends in Plant Science*, 3 (4): 131-135.
Jansen, M. A. K. & van den Noort, R. E. (2000). Ultraviolet-B radiation induces complex alterations in stomatal behaviour. *Physiologia Plantarum*, 110 (2): 189-194.
Jenkins, G. I. (2009). Signal transduction in responses to UV-B radiation. *Annual Review of Plant Biology*, 60: 407-31.
Jenkins, G. I. (2014). The UV-B photoreceptor UVR8: From structure to physiology. *The Plant Cell Online*, 26 (1): 21-37.
Jeon, M.-W., Ali, M. B., Hahn, E.-J. & Paek, K.-Y. (2006). Photosynthetic pigments, morphology and leaf gas exchange during *ex vitro* acclimatization of micropropagated CAM *Doritaenopsis* plantlets under relative humidity and air temperature. *Environmental and Experimental Botany*, 55: 183-194.
Johanson, U., Gehrke, C., Björn, L. O. & Callaghan, T. V. (1995). The effects of enhanced UV-B radiation on the growth of dwarf shrubs in a subarctic heathland. *Functional Ecology*, 9: 713-719.
Kakani, V. G., Raja Reddy, K., Zhao, D. & Mohammed, A. R. (2003). Effects of ultraviolet-B radiation on cotton (*Gossypium hirsutum* L.) morphology and anatomy. *Annals of Botany*, 91 (7): 817-826.
Kerstiens, G. (1994). Effects of low light intensity and high air humidity on morphology and permeability of plant cuticles, with special respect to plants cultured in vitro. In Lumsden, P. J., Nicholas, J. R. & Davies, W. J. (eds) *Physiology, Growth and Development of Plants in Culture*, pp. 132-142: Springer Netherlands.
Koch, K., Hartmann, K. D., Schreiber, L., Barthlott, W. & Neinhuis, C. (2006). Influences of air humidity during the cultivation of plants on wax chemical composition, morphology and leaf surface wettability. *Environmental and Experimental Botany*, 56 (1): 1-9.
Koti, S., Raja Reddy, K., Kakani, V. G., Zhao, D. & Gao, W. (2007). Effects of carbon dioxide, temperature and ultraviolet-B radiation and their interactions on soybean (*Glycine max* L.) growth and development. *Environmental and Experimental Botany*, 60: 1-10.
Kraus, T. E., Fletcher, R. A., Evans, R. C. & Pauls, K. P. (1995). Paclobutrazol enhances tolerance to increased levels of UV-B radiation in soybean (*Glycine max*) seedlings. *Canadian Journal of Botany*, 73 (6): 797-806.
Lambers, H., Chapin, F. S. I. & Pons, T. J. (2008). *Plant Physiological Ecology*. 2nd ed. New York, USA: Springer Science + Business Media, LLC.
Lee, T. A., Ketring, D. L. & Powell, R. D. (1972). Flowering and growth response of peanut plants (*Arachis hypogaea* L. var. Starr) at two levels of relative humidity. *Plant Physiology*, 49 (2): 190-193.
Leuschner, C. (2002). Air humidity as an ecological factor for woodland herbs: Leaf water status, nutrient uptake, leaf anatomy, and productivity of eight species grown at low or high vpd levels. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 197 (4): 262-274.
Leys, C. & Schumann, S. (2010). A nonparametric method to analyze interactions: The adjusted rank transform test. *Journal of Experimental Social Psychology*, 46: 684-688.

Lingakumar, K., Amudha, P. & Kulandaivelu, G. (1999). Exclusion of solar UV-B (280–315 nm) radiation on vegetative growth and photosynthetic activities in *Vigna unguiculata* L. *Plant Science*, 148 (2): 97-103.
Liu, L., Gitz, D. C. & McClure, J. W. (1995). Effects of UV-B on flavonoids, ferulic acid, growth and photosynthesis in barley primary leaves. *Physiologia Plantarum*, 93 (4): 725-733.
Lydon, J., Teramura, A. H. & Summers, E. G. (1986). Effects of ultraviolet-B radiation on the growth and productivity of field grown soybean. In Worrest, R. & Caldwell, M. (eds) NATO ASI Series, vol. 8 *Stratospheric Ozone Reduction, Solar Ultraviolet Radiation and Plant Life*, pp. 313-325: Springer Berlin Heidelberg.
Mackerness, S. A.-H.-., Surplus, S. L., Jordan, B. R. & Thomas, B. (1998). Effects of supplementary ultraviolet-B radiation on photosynthetic transcripts at different stages of leaf development and light levels in pea (*Pisum sativum* L.): Role of active oxygen species and antioxidant enzymes. *Photochemistry and Photobiology*, 68 (1): 88-96.
Mahdavian, K., Ghorbanli, M. & Kalantari, K.-M. (2008). The effects of ultraviolet radiation on on the contents of chlorophyll, flavonoid, anthocyanin and proline in *Capsicum annuum*. *Turkish Journal of Botany*, 32: 25-33.
Martinez-Luscher, J., Sanchez-Diaz, M., Delrot, S., Aguirreolea, J., Pascual, I. & Gomes, E. (2014). Ultraviolet-B radiation and water deficit interact to alter flavonol and anthocyanin profiles in grapevine berries through transcriptomic regulation. *Plant and Cell Physiology*, 55 (11): 1925-36.
Martinez, C., Pons, E., Prats, G. & Leon, J. (2004). Salicylic acid regulates flowering time and links defence responses and reproductive development. *The Plant Journal*, 37 (2): 209-17.
Meijkamp, B. B., Doodeman, G. & Rozema, J. (2001). The response of *Vicia faba* to enhanced UV-B radiation under low and near ambient PAR levels. In Rozema, J., Manetas, Y. & Björn, L.-O. (eds) Advances in Vegetation Science, vol. 18 *Responses of Plants to UV-B Radiation*, pp. 135-146: Springer Netherlands.
Middleton, E. M. & Teramura, A. H. (1993). Potential errors in the use of cellulose diacetate and mylar filters in UV-B radiation studies *Photochemistry and Photobiology*, 57 (4): 744-751.
Moe, R. & Heins, R. D. (1990). Control of plant morphogenesis and flowering by light quality and temperature. *Acta Horticulturae (ISHS)*, 272 (81-90).
Moe, R., Fjeld, T. & Mortensen, L. M. (1992a). Stem elongation and keeping quality in poinsettia (Euphorbia pulcherrima Willd.) as affected by temperature and supplementary lighting. *Scientia Horticulturae*, 50 (1–2): 127-136.
Moe, R., Glomsrud, N., Bratberg, I. & Valsø, S. (1992b). Control of plant height in poinsettia by temperature drop and graphical tracking. *Acta Horticulturae (ISHS)*, 327: 41-48.
Mortensen, L. M. (1986). Effect of relative humidity on growth and flowering of some greenhouse plants. *Scientia Horticulturae*, 29 (4): 301-307.
Mortensen, L. M. & Gislerød, H. R. (1990). Effects of air humidity and supplementary lighting on foliage plants. *Scientia Horticulturae*, 44 (3–4): 301-308.
Mortensen, L. M. & Fjeld, T. (1998). Effects of air humidity, lighting period and lamp type on growth and vase life of roses. *Scientia Horticulturae*, 73 (4): 229-237.
Mortensen, L. M. & Gislerød, H. R. (1999). Influence of air humidity and lighting period on growth, vase life and water relations of 14 rose cultivars. *Scientia Horticulturae*, 82 (3–4): 289-298.
Mortensen, L. M. (2000). Effects of air humidity on growth, flowering, keeping quality and water relations of four short-day greenhouse species. *Scientia Horticulturae*, 86 (4): 299-310.
Mpoloka, S. W. (2008). Effects of prolonged UV-B exposure in plants. *African Journal of Biotechnology*, 7 (25): 4874-4883.
Murali, N. S. & Saxe, H. (1984). Effects of ultraviolet-C radiation on net photosynthesis, transpiration and dark respiration of *Spathiphyllum wallisii*. *Physiologia Plantarum*, 60 (2): 192-196.
Nedunchezhian, N. & Kulandaivelu, G. (1997). Changes induced by ultraviolet-B (280–320 nm) radiation to vegetative growth and photosynthetic characteristics in field grown *Vigna unguiculata* L. *Plant Science*, 123 (1–2): 85-92.
Negash, L. & Björn, L. O. (1986). Stomatal closure by ultraviolet radiation. *Physiologia Plantarum*, 66 (3): 360-364.

Nogués, S., Allen, D. J., Morison, J. I. L. & Baker, N. R. (1998). Ultraviolet-B radiation effects on water relations, leaf development, and photosynthesis in droughted pea plants. *Plant Physiology*, 117 (1): 173-181.
Nogués, S., Allen, D. J., Morison, J. I. L. & Baker, N. R. (1999). Characterization of stomatal closure caused by ultraviolet-B radiation. *Plant Physiology*, 121 (2): 489-496.
North Carolina State University Department of Horticultural Science. (2014a). *Bravo Bright Red*. Poinsettia Trials: North Carolina State University and A&T State University Cooperative Extension. Available at: https://trials.ces.ncsu.edu/poinsettias/variety/bravo-bright-red/ (accessed: 27-04-2015).
North Carolina State University Department of Horticultural Science. (2014b). *Infinity Red*. Poinsettia Trials: North Carolina State University and A&T State University Cooperative Extension. Available at: https://trials.ces.ncsu.edu/poinsettias/variety/infinity-red/ (accessed: 27-04-2015).
Oh, W., Cheon, I. H., Kim, K. S. & Runkle, E. S. (2009). Photosynthetic daily light integral influences flowering time and crop characteristics of *Cyclamen persicum*. *HortScience*, 44 (2): 341-344.
Pramuk, L. A. & Runkle, E. S. (2005a). Modeling growth and development of *Celosia* and *Impatiens* in response to temperature and photosynthetic daily light integral. *HortScience*, 130 (6): 813-818.
Pramuk, L. A. & Runkle, E. S. (2005b). Photosynthetic daily light integral during the seedling stage influences subsequent growth and flowering of *Celosia*, *Impatiens*, *Salvia*, *Tagetes*, and *Viola*. *HortScience*, 40 (5): 1336-1339.
Q-Lab Corporation. (2011). *Technical Bulletin LU-8051*: Q-Lab Corporation (accessed: 29-04-2015).
Qaderi, M. M., Yeung, E. C. & Reid, D. M. (2008). Growth and physiological responses of an invasive alien species, Silene noctiflora, during two developmental stages to four levels of ultraviolet-B radiation. *Ecoscience*, 15 (2): 150-159.
Rajapakse, N. C. & Kelly, J. W. (1992). Regulation of chrysanthemum growth by spectral filters. *HortScience*, 117 (3): 481-485.
Rajapakse, N. C., Young, R. E., McMahon, M. J. & Oi, R. (1999). Plant height control by photoselective filters: Current status and future prospects. *HortTechnology*, 9 (4): 618-624.
Rezaei Nejad, A. & Van Meeteren, U. (2005). Stomatal response characteristics of *Tradescantia virginiana* grown at high relative air humidity. *Physiologia Plantarum*, 125 (3): 324-332.
Rezaei Nejad, A. & van Meeteren, U. (2007). The role of abscisic acid in disturbed stomatal response characteristics of *Tradescantia virginiana* during growth at high relative air humidity. *Journal of Experimental Botany*, 58 (3): 627-636.
Rezaei Nejad, A. & van Meeteren, U. (2008). Dynamics of adaptation of stomatal behaviour to moderate or high relative air humidity in *Tradescantia virginiana*. *Journal of Experimental Botany*, 59 (2): 289-301.
Rizzini, L., Favory, J.-J., Cloix, C., Faggionato, D., O'Hara, A., Kaiserli, E., Baumeister, R., Schäfer, E., Nagy, F., Jenkins, G. I., et al. (2011). Perception of UV-B by the *Arabidopsis* UVR8 Protein. *Science*, 332 (6025): 103-106.
Roro, A. G. (2015). *Impact of UV radiation on plant growth and development in different climatic regimes*: Norwegian University of Life Sciences, Department of Plant Sciences.
Rozema, J., Boelen, P., Solheim, B., Zielke, M., Buskens, A., Doorenbosch, M., Fijn, R., Herder, J., Callaghan, T., Björn, L., et al. (2006). Stratospheric ozone depletion: high arctic tundra plant growth on Svalbard is not affected by enhanced UV-B after 7 years of UV-B supplementation in the field. In Rozema, J., Aerts, R. & Cornelissen, H. (eds) Tasks for vegetation science, vol. 41 *Plants and Climate Change*, pp. 121-136: Springer Netherlands.
Sampath-Wiley, P. & Jahnke, L. S. (2011). A new filter that accurately mimics the solar UV-B spectrum using standard UV lamps: the photochemical properties, stabilization and use of the urate anion liquid filter. *Plant, Cell & Environment*, 34 (2): 261-269.
Santamaria, J. M., Davies, W. J. & Atkinson, C. J. (1993). Stomata of micropropagated *Delphinium* plants respond to ABA, CO2, light and water potential, but fail to close fully. *Journal of Experimental Botany*, 44 (1): 99-107.

Savaldi-Goldstein, S., Peto, C. & Chory, J. (2007). The epidermis both drives and restricts plant shoot growth. *Nature*, 446 (7132): 199-202.
Singh, M., Singh, S. & Agrawal, S. B. (2012). Intraspecific responses of six cultivars of wheat (*Triticum aestivum* L.) to supplemental ultraviolet-B radiation under field conditions. *Acta Physiologiae Plantarum*, 34 (1): 65-74.
Slatnar, A., Mikulic-Petkovsek, M., Veberic, R., Stampar, F. & Schmitzer, V. (2013). Anthocyanin and chlorophyll content during poinsettia bract development. *Scientia Horticulturae*, 150: 142-145.
Stapleton, A. E. & Walbot, V. (1994). Flavonoids can protect maize DNA from the induction of ultraviolet radiation damage. *Plant Physiology*, 105 (3): 881-889.
Strid, Å., Chow, W. & Anderson, J. (1994). UV-B damage and protection at the molecular level in plants. *Photosynthesis Research*, 39 (3): 475-489.
Strømme, E. (1994). *The Scientific Basis of Poinsettia Production*: Agricultural University of Norway.
Surabhi, G.-K., Reddy, K. R. & Singh, S. K. (2009). Photosynthesis, fluorescence, shoot biomass and seed weight responses of three cowpea (*Vigna unguiculata* (L.) Walp.) cultivars with contrasting sensitivity to UV-B radiation. *Environmental and Experimental Botany*, 66 (2): 160-171.
Suthaparan, A., Stensvand, A., Solhaug, K. A., Torre, S., Mortensen, L. M., Gadoury, D. M., Seem, R. C. & Gislerød, H. R. (2012). Suppression of powdery mildew (*Podosphaera pannosa*) in greenhouse roses by brief exposure to supplemental UV-B radiation. *Plant Disease*, 96 (11): 1653-1660.
Suthaparan, A., Stensvand, A., Solhaug, K. A., Torre, S., Telfer, K. H., Ruud, A. K., Mortensen, L. M., Gadoury, D. M., Seem, R. C. & Gislerød, H. R. (2014). Suppression of cucumber powdery mildew by supplemental UV-B radiation in greenhouses can be augmented or reduced by background radiation quality. *Plant Disease*, 98 (10): 1349-1357.
Taiz, L. & Zeiger, E. (2010). *Plant Physiology*. Fifth ed. MA, USA: Sinauer Associates, Inc.
Tanaka, Y., Sano, T., Tamaoki, M., Nakajima, N., Kondo, N. & Hasezawa, S. (2005). Ethylene inhibits abscisic acid-induced stomatal closure in *Arabidopsis*. *Plant Physiology*, 138: 2337-2343.
Teramura, A. & Sullivan, J. (1994). Effects of UV-B radiation on photosynthesis and growth of terrestrial plants. *Photosynthesis Research*, 39 (3): 463-473.
Teramura, A. H., Ziska, L. H. & Sztein, A. E. (1991). Changes in growth and photosynthetic capacity of rice with increased UV-B radiation. *Physiologia Plantarum*, 83 (3): 373-380.
Torre, S. & Fjeld, T. (2001). Water loss and postharvest characteristics of cut roses grown at high or moderate relative air humidity. *Scientia Horticulturae*, 89 (3): 217-226.
Torre, S., Fjeld, T., Gislerød, H. R. & Moe, R. (2003). Leaf anatomy and stomatal morphology of greenhouse roses grown at moderate or high air humidity. *HortScience*, 128 (4): 598-602.
Tossi, V., Lamattina, L. & Cassia, R. (2009). An increase in the concentration of abscisic acid is critical for nitric oxide-mediated plant adaptive responses to UV-B irradiation. *New Phytologist*, 181 (4): 871-879.
Tossi, V. E., Lamattina, L., Jenkins, G. & Cassia, R. (2014). UV-B-induced stomatal closure in Arabidopsis is regulated by the UVR8 photoreceptor in an NO-dependent mechanism. *Plant Physiology*.
Wargent, J. J., Gegas, V. C., Jenkins, G. I., Doonan, J. H. & Paul, N. D. (2009). UVR8 in *Arabidopsis thaliana* regulates multiple aspects of cellular differentiation during leaf development in response to ultraviolet B radiation. *New Phytologist*, 183 (2): 315-26.
White, A. L. & Jahnke, L. S. (2004). Removing UV-A and UV-C radiation from UV-B fluorescent lamp emissions. Differences in the inhibition of photosynthesis in the marine alga *Dunaliella tertiolecta* using chromate versus cellulose acetate–polyester Filters. *Photochemistry and Photobiology*, 80 (2): 340-345.
Wright, L. A. & Murphy, T. M. (1982). Short-wave ultraviolet light closes leaf stomata. *American Journal of Botany*, 69 (7): 1196-1199.

Zvezdanović, J., Cvetić, T., Veljović-Jovanović, S. & Marković, D. (2009). Chlorophyll bleaching by UV-irradiation *in vitro* and *in situ*: Absorption and fluorescence studies. *Radiation Physics and Chemistry*, 78 (1): 25-32.



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