UV radiation as a tool to control growth, morphology and transpiration of poinsettia (*Euphorbia pulcherrima*) in variable aerial environments

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Abstract

Greenhouse production of poinsettia calls for strict control of morphological parameters, which may be achieved through the use of chemical growth retardants. Use of such chemicals is becoming restricted thus alternative methods for growth control are needed. Here the effects of UV radiation were tested on *Euphorbia pulcherrima* (Willd ex. Klotzch) in controlled environment under moderate (60%) and high (90%) relative air humidity (RH), to determine the potential to control plant morphology. Vegetative plants ('Christmas Feelings') received UV during the dark period, while two generative cultivars, one strong growing phenotype 'Infinity Red' ('IR') and one more compact phenotype 'Bravo Bright Red' ('BBR'), received UV at the end of the light period (EOD). The morphology of vegetative plants was mainly affected by RH rather than UV radiation. Generative plants were also strongly affected by RH, though both cultivars showed reduced plant

diameter, shoot biomass, leaf area, and bract area when exposed to UV, as well as increased leaf chlorophyll content, though responses to UV were stronger in moderate RH compared to high RH. Transpiration of leaves and bracts was mainly affected by RH not UV, and photosynthesis and production time were not affected by either RH or UV. We conclude that UV radiation is a potential tool to grow more compact plants, though its effects are partially determined by the aerial environment.

Keywords: Ornamental, plant production, growth regulation, stomata, Christmas flower.

1. Introduction

Poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) is an important ornamental potted plant species produced in greenhouses for the Christmas season and valued for its intensely coloured bracts. Plant growth control is important in poinsettia production and may be accomplished using chemical growth retardants (Alem et al. 2015). While non-chemical production methods and climate manipulation for growth control are in wide use in production today, further investigation into novel techniques is required as chemical restrictions and environmental protection become increasingly important (De Castro et al. 2004; Sørensen & Danielsen 2006). Methods such as diurnal temperature drops, lower day- than night- temperature (negative DIF) regimes (Myster & Moe 1995) and light quality manipulation using light emitting diodes (LEDs) (Islam et al. 2012; Islam et al. 2014) have been found to prevent excessive height in poinsettia. Light quality manipulation is increasingly used as a means of minimising chemical growth retardants in production systems, and the potential use of UV radiation in the same way remains little investigated. In a previous study on the effects of UV radiation on poinsettia, Torre et al. (2012)

found a reduction in internode elongation and an increase in branching in response to a low dose of UV-B radiation given during the dark period. The study was performed on vegetative plants under long day (LD) conditions, yet testing the influence of UV on generative plants under SD conditions is important to evaluate its effect on production time, as it has previously been shown that UV-B can affect flowering (Martínez et al. 2004).

UV radiation, as UV-A (315-400 nm), UV-B (280-315 nm) and UV-C (<280 nm), has pleiotropic effects on plant growth and development (Frohnmeyer & Staiger 2003; Mackerness et al. 1998; Strid et al. 1994; Wargent et al. 2009). Plant morphological responses to UV-B radiation have been thoroughly investigated for a large range of species under field-, greenhouse- and controlled environment conditions, as reported in several reviews. Despite variations in study conditions and species,, 'keystone' UV radiation responses have been identified, such as plant height and leaf area reductions, and increased content of UV screening phenolic compounds (Wargent 2016). Further commonly reported responses to UV radiation include increased leaf thickness, reduced plant biomass, reduced chlorophyll content, and visible damage such as leaf curling and bronzing (Baroniya et al. 2011; Deckmyn et al. 1994; Frohnmeyer & Staiger 2003; Nogués et al. 1998).

Several studies have focused on the effects of UV-B radiation on stomatal behaviour, with often contradictory results, though the greater consensus report stomatal closure upon plant exposure to UV-B radiation (He et al. 2005; Negash & Björn 1986; Nogués et al. 1999; Tossi et al. 2009; Tossi et al. 2014). Jansen and Van Den Noort (2000) attribute the disagreement in reported findings to the initial metabolic state of the guard cells when UV-B radiation is applied, reporting that in their study UV-B radiation served to enhance the initial state of the guard cells, that is, either enhance stomatal opening or closing. Stomatal behaviour and plant water relations

are important in plant production systems, as control of water relations contributes to minimising production expenses, as well as optimising post-harvest quality (Arve et al. 2013).

High relative air humidity (RH) regimes are often employed in 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 using closed systems to reduce heat loss (Mortensen 2000). A diverse range of morphological responses to high RH has been shown in controlled environment studies, such as increased stem elongation and increased leaf area (Hovenden et al. 2012; Jeon et al. 2006; Leuschner 2002; Torre et al. 2003). Increased leaf area in plants grown at high RH has been associated with changes in photosynthesis and carbon metabolism (Grange & Hand 1987; Jeon et al. 2006). Thinner leaves at high RH reported by Torre et al. (2003) was attributed to a reduction in epidermis thickness along with smaller spongy- and palisade mesophyll cells. Tall plants with thin leaves are undesirable in commercial plant production, where compact and robust plants are required. Additionally, production in high RH can have a direct negative effect on post-harvest keeping quality due to high postharvest water loss and lower stress tolerance, as seen in ornamentals and cut flowers (Mortensen & Fjeld 1998; Mortensen & Gislerød 1999; Mortensen 2000; Torre & Fjeld 2001; Torre et al. 2003).

The aim of the study was to investigate the responses of poinsettia to artificial UV radiation grown in moderate and high humidity for the purpose of exploring potential improvement of production methods. Since many greenhouses have cladding or glazing material that does not transmit UV radiation and natural UV radiation is low during the period when poinsettias are produced, the use of UV lamps forms an alternative means of providing UV radiation in commercial production. We investigated the hypotheses that exposure of the plants to UV radiation

would a) combat the morphological impacts of high RH and induce a more compact, robust growth form and b) improve plant water relations during production in a high RH environment.

2. Materials and Methods

2.1. Experiment 1: Vegetative growth of poinsettia

Cuttings of poinsettia '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), for an initial growth period. In addition to natural light, the plants received 100 µmol m^{-2} s^{-1} PAR from high pressure sodium (HPS) lamps (Osram NAV T-400W, Munich, Germany), measured using a Li-Cor quantum sensor connected to a Li-Cor Model L1-250 light meter (Li-Cor Inc., Lincoln, NE, USA). The plants were pinched over 3-4 leaves and two weeks later, when the new shoots were approximately three centimetres, the plants were moved to controlled environment growth chambers for UV exposure.

The plants were subjected to long day (LD) treatment, with a 20/4 h light/dark photoperiod regime receiving PAR radiation at 150 ± 10 µmol m^{-2} s^{-1} from HPS lamps. This gave a daily light integral (DLI) of 10.8 mol m^{-2} d^{-1}. Temperature was maintained at 21°C ± 1°C and ambient CO_2 (approximately 400 ppm) in all chambers by a PRIVA system. The plants were grown in a factorial design using four growth chambers (Table 1). Two levels of RH treatment, moderate (60%) or high (90%) RH, and two levels of UV treatment, either not exposed (-UV) or exposed (+UV) to 0.15 W m^{-2} UV radiation (at plant height) for 40 minutes in the middle of the dark period, were

combined to create four treatment combinations (Table 1). The Green weighting spectrum for DNA damage (Green et al. 1974), normalised to 1 at 300 nm, was used to estimate biologically effective UV-B at 0.22 W m^{-2}. Individual plants were the unit of replication within each treatment (n = 5 per treatment). The plants were rotated in the chambers once a day.

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). The UV sensor was calibrated using an Optronic OL756 Spectroradiometer (Optronic Laboratories, Inc., Florida, USA). The lamps produced mostly radiation in the UV-B range (280-315 nm) with some radiation in the UV-A (315-400 nm) and the UV-C (< 280 nm) ranges (Figure 1).

Cellulose di-acetate is often used to block wavelengths below 295 nm to simulate solar UV-B. However, unscreened fluorescent lamps were chosen for this investigation as the study was not geared to simulate solar UV, and was rather to investigate the practical potential of such a light source in commercial poinsettia production.

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), EC level 1.5 mS cm^{-1}.

The plants were pinched again when the shoots were approximately 10 cm long, and four shoots were allowed to develop per plant. After 56 days of LD treatment plant height from the rim of the pot to the shoot apical meristem, plant diameter (as the average of two perpendicular cross-sectional measurements), shoot length, petiole length (as average of the three longest petioles on

137 the two longest shoots) and leaf area, using a LI-3100 Area Meter (Li-Cor, Inc., Lincoln, Nebraska,
138 USA), were measured. Additionally, the total number of leaves was counted, the fresh mass (FM)
139 and dry mass (DM) of the leaves were weighed, and the stem of the longest shoot was measured.
140 The leaves and stems were dried for at least three days in a desiccation cupboard at 60°C. Specific
141 leaf area (SLA) was calculated by dividing leaf area by leaf DM. Average internode length (mean
142 leaves per shoot/mean shoot length) was calculated as well as the percentage of biomass found in
143 shoots and leaves (100*shoot or leaf DM/total DM).
144
145 ***2.2. Experiment 2: Generative growth of poinsettia***
146 Cuttings of two poinsettia cultivars, 'Infinity Red' ('IR') and 'Bravo Bright Red' ('BBR') (*n*
147 = 40 for each cultivar), were obtained in June 2014 from GASA Young Plants (GASA GROUP
148 Denmark A/S, Odense, Denmark). The rooted cuttings were pinched above four leaves and potted
149 in 12 cm pots with Sphagnum peat growth medium, 6% ash, pH 5.0-6.0 (Degernes Torvstrøfabrikk
150 AS, Degernes, Norway). The plants were transferred to controlled growth chambers and exposed
151 to long day (LD) treatment (20/4 h light/dark photoperiod regime), 22 ± 1°C, ambient CO_2 and 70
152 ± 5% RH for 16 days prior to the short day (SD) treatments. Light was supplied at 150 ± 10 µmol
153 m^{-2} s^{-1} by HPS lamps (Osram NAV T-400W, Munich, Germany).
154 Ten plants from each cultivar were placed in each chamber (setup shown in Table 1). EOD
155 UV radiation overlapped with the light period for five minutes. UV radiation was provided by
156 unscreened fluorescent tubes, as in Expt. 1. Temperature was maintained at 22 ± 1°C, RH at either
157 60 or 90 ± 5% and ambient CO_2 (approximately 400 ppm) by a PRIVA system. The plants were
158 watered as in Expt. 1.

159 The setup of the experiments was chosen to mimic that used in the prevention of fungal
160 diseases (Suthaparan et al. 2012; Suthaparan et al. 2014), though due to the need for SD conditions
161 to induce flowering in the plants in Expt. 2 UV radiation could not be given as a dark period
162 interruption and was instead provided as EOD radiation. UV dose was chosen based on findings
163 from previous experiments (Torre et al., 2012, Suthaparan et al., 2012) to be in accordance with
164 the aims of this study. Previous work on poinsettia indicated sensitivity even to low doses of UV,
165 while previous work on fungal disease (Suthaparan et al., 2012) indicated an effect of such a low
166 dose in the prevention of fungal disease spread.

167 The plants were pinched when the shoots were approximately 10 cm long, 16 days after the
168 start of SD treatment (ASD) and three shoots were allowed to develop per plant. Destructive
169 measurements were taken at the appearance of visible cyathia, 58 days ASD. Plant height from the
170 rim of the pot to the shoot apical meristem and plant diameter (as the average of two perpendicular
171 cross-sectional measurements) were measured for each plant, while shoot length, petiole length of
172 the three longest leaves and bracts, leaf and bract area, and FM and DM of shoots, leaves and
173 bracts were all measured for each shoot. The number of leaves and bracts was counted for each
174 shoot. Specific leaf area (SLA) and specific bract area (SBA) were calculated by dividing either
175 the leaf or bract area by leaf or bract DM respectively. Average internode length (mean leaves plus
176 bracts per shoot/mean shoot length) was calculated, as well as the percentage of biomass found in
177 shoots, leaves and bracts (100*shoot, leaf or bract DM/total DM). Additionally, relative
178 chlorophyll content measurements, using a CL-01 Chlorophyll Content Meter (Hansatech
179 Instruments Ltd., Norfolk, UK), were conducted. Time to flowering (visible cyathia) was recorded.

180 Measurements of plant photosynthesis and transpiration rates were taken in the growth
181 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). All gas exchange measurements taken on leaves were performed on the fourth or fifth leaf from the base of the plant – mature and undamaged. Two measurements per leaf were taken from five plants per treatment, in both light and dark conditions. Measurements from bracts were taken in the same way, using fully expanded, completely red bracts. CO_2 concentration in the cuvette was maintained at ambient levels (400 ppm) and cuvette temperature at 21°C. Ambient light at 150 ± 10 μmol m^{-2} s^{-1}, provided by HPS lamps, was used during measurement. Additional conductance measurements were taken using an AP4 Porometer (Delta-T Devices Ltd., Cambridge, UK).

2.3. 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. Due to the factorial nature of the setup, testing of the effects of RH, UV and RHxUV interaction on the plants 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, and for interaction effects using Adjusted Rank Transform tests. In cases if heteroscedasticity data were analysed using a One-Way Analysis of Means not assuming equal variance.

3. Results

3.1. Experiment 1: Vegetative growth of Poinsettia

204 Growth and morphology of poinsettia 'CF' grown in LD conditions was significantly affected
205 by RH, yet UV radiation only had significant effects on two growth variables (Table 2). Leaves
206 from +UV plants had 20% and 11% smaller leaf area than –UV plants in 60% and 90% RH
207 respectively. A similar effect was found in leaf petiole length, where +UV plants were 25% and
208 13% shorter than –UV plants in 60% and 90% RH respectively. Plants grown in high RH had a
209 13-20% greater height and 8-18% greater diameter compared to moderate RH. Similarly, increases
210 in shoot length, number of leaves per shoot, leaf area, SLA and petiole length, were found in plants
211 grown at high RH compared to moderate RH (Table 2). A19-21% decrease in internode length
212 was found in plants grown at high RH plants compared to moderate RH though the number of
213 internodes was significantly increased. An interaction between RH and UV was found for the
214 number of leaves per shoot, which were 13% fewer +UV plants compared to –UV plants in 60%
215 RH and not different in 90% RH (Table 2).
216 No significant effects of RH or UV on total shoot biomass were found (results not shown).
217 Plants grown in moderate RH allocate ~70% DM to leaves and ~30% DM to stems. However,
218 plants grown in high RH allocate ~50% DM to leaves and stems. UV exposure did not have a
219 significant effect on DM distribution between organs.
220
221 ### *3.2. Experiment 2: Generative growth of poinsettia*
222 #### *3.2.1.* Morphological parameters of poinsettia 'Infinity Red'
223 Plants in high RH, responded to UV exposure with 8-10% increased extension growth
224 compared to the other treatments (Table 3). Shoot length, the number of leaves per stem and the
225 number of bracts per stem all showed highly significant interaction effects between RH and UV
226 (Table 3). Plants grown in high RH and exposed to UV had 18-24% longer shoots, 14-19% more

leaves per shoot and 10-21% more bracts per shoot compared to the other treatments. In moderate RH, UV exposure had no effect on shoot length or the number of leaves per shoot. Plants grown in high RH had 6% (+UV) and 10% (-UV) longer internodes than plants grown in moderate RH.

In both plant diameter (Table 4) and the number of bracts per stem (Table 3), the direction and magnitude of the effects of UV were influenced by the RH level at which plants were grown. The interaction between high RH and UV exposure resulted in an increase in both leaf and bract petiole lengths in comparison to -UV plants (18% and 22% respectively), though the plants grown at high RH had shorter leaf and bract petioles than the plants grown at moderate RH regardless of UV exposure (Table 3). No effect of UV exposure was seen in leaf and bract petiole lengths at moderate RH.

Plants exposed to UV at both RH levels showed decreased leaf area compared to -UV plants (44% and 38% for moderate and high RH respectively), and –UV plants had a 17% smaller leaf area in high RH compared to moderate RH (Table 4). Exposure to UV in high RH resulted in plants with an 8% smaller bract area compared to -UV plants, yet moderate RH plants had a 40% and 15% greater bract area than high RH in-UV and +UV plants respectively (Table 4). In high RH, plants exposed to UV had 6-15% thicker leaves (lowest SLA) compared to the other treatments, and in moderate RH +UV plants had 10% greater leaf thickness compared to –UV plants (Table 4). In high RH, +UV plants had 19% thinner bracts compared to –UV plants, though plants grown at moderate RH had thinner bracts than plants grown at high RH regardless of UV exposure (Table 4). A one-day delay in open cyathia was found for –UV plants grown at high RH (data not shown). Chlorophyll content was significantly higher in +UV plants compared to –UV plants at both RH levels (data not shown).

3.2.2. Morphological parameters of poinsettia ‘Bravo Bright Red’

Neither plant height nor internode length in poinsettia ‘BBR’ showed any effect of RH or UV (Table 3). The combination of high RH and UV resulted in plants with the longest shoots and the greatest number of leaves per stem compared to other treatments (Table 3). However, the interaction effect between moderate RH and UV resulted in plants with 10% shorter shoots and 10% fewer leaves compared to –UV plants. High RH combined with UV exposure resulted in plants with a slightly higher number of bracts per stem compared to –UV plants. UV-exposed plants grown at moderate RH had 14% more bracts per stem than UV-exposed plants grown at high RH (Table 3).

In high RH exposure to UV resulted in a 4% greater plant diameter, while in moderate RH the same UV exposure resulted in a 13% decrease in diameter, compared to -UV plants (Table 4). Additionally, in high RH exposure to UV resulted in 25% and 41% longer petioles in both leaves and bracts respectively, compared to –UV plants, though plants grown at moderate RH had longer leaf and bract petioles than plants grown at high RH regardless of UV exposure (Table 3).

UV exposure resulted in a 38% and 19% decrease in leaf area compared to –UV plants at moderate and high RH respectively, and –UV plants grown at high RH had smaller leaves than –UV plants grown at moderate RH (Table 4). In high RH UV exposure resulted in a 38% increase in bract area compared to –UV plants, while UV exposure in moderate RH resulted in a 10% decrease in bract area compared to –UV plants (Table 4). Additionally, plants grown at high RH had smaller bracts than plants grown at moderate RH regardless of UV exposure. In high RH UV exposure resulted in a 17% decrease in leaf thickness compared to –UV plants, while in moderate RH UV exposure resulted in a 6% increase in leaf thickness compared to –UV plants (Table 4). UV exposure resulted in a 21% and 10% decrease in bract thickness at high and moderate RH

respectively, while –UV plants grown at high RH had thicker bracts than –UV plants grown at moderate RH (Table 4). A one-day delay in open cyathia was found for –UV plants grown at high RH (data not shown). Chlorophyll content increased significantly in +UV plants compared to –UV plants at both RH levels (data not shown).

3.2.3. Shoot DM distribution

In the strong growing phenotype ‘IR’, plants exposed to UV at both RH levels showed a significant reduction in total biomass compared to -UV plants (Figure 2), though the reduction was stronger in moderate RH. Such was not the case in the more compact phenotype ‘BBR’, where exposure to UV caused a reduction in total biomass only in moderate RH (Figure 2). Furthermore, ‘BBR’ plants grown in high RH had reduced total biomass compared to moderate RH -UV plants, regardless of UV exposure.

Both ‘IR’ and ‘BBR’ plants allocated a greater proportion of total biomass to stems when grown in high RH (Figure 2). A decrease in leaf DM in +UV plants compared to –UV plants was seen at both levels of RH and more strongly in ‘BBR’ compared to ‘IR’. However, no effects of UV were seen in shoot DM distribution in either phenotype.

3.2.4. Effects of RH and UV on leaf and bract transpiration

Leaf conductance measured on plants outside the chambers (40-50% RH) showed an increase in both ‘BBR’ and ‘IR’ plants when grown in high RH compared to moderate RH (Table 5). However, UV exposure did not significantly affect leaf conductance in either of the cultivars. Neither RH nor UV had an effect on bract conductance in ‘IR’ plants, while in ‘BBR’ plants bract

conductance was higher when grown in high RH than in moderate RH, regardless of UV exposure (Table 5). No effect of RH or UV was seen on leaf photosynthesis (Table 5).

4. Discussion

4.1. Growth and morphological responses to UV radiation

Growth and morphological responses to different combinations of RH and UV radiation were tested in vegetative 'CF' and generative 'IR' and 'BBR' poinsettia plants grown in growth chambers. In both experiments, UV exposure brought about changes in growth and morphology. However, the effect of UV was dependent on ontogenetic stage, air humidity during growth and cultivar.

Vegetative 'CF' plants (Expt. 1) in general showed a stronger growth response to RH than to UV radiation (Table 2). Increased RH promoted stem and petiole elongation and leaf expansion as shown previously (Mortensen 2000). Leaf growth parameters (leaf area and petiole length) were the only parameters to respond to UV and were reduced compared to unexposed plants. UV did not affect stem or internode lengths in this experiment as previously shown in an experiment with vegetative poinsettia (Torre et al. 2012). In their experiment, Torre et al. (2012) exposed plants to 1 h of UV during the night using unscreened UV-B tubes, which resulted in significantly reduced internode length compared to control plants. The growth and UV conditions used in the experiments performed here were chosen for several reasons. The initial growth conditions were chosen so as to mimic conditions in commercial production. Torre et al. (2012) used a UV dose of either 0.1 or 0.2 W m^{-2} for 1 h in the middle of the dark period, and found that plants exposed to the higher dose showed signs of injury. Furthermore, Suthaparan et al. (2012) indicated an effect of 0.1 W m^{-2} UV radiation in combatting pathogens. Given these previous findings, we postulated

318 that 0.15 W m^{-2} UV would not induce injury, yet may additionally be useful in pathogen control
319 in poinsettia. In comparison to many studies this is considered a low UV dose, for example: Craver
320 et al. (2014) exposed their sweet potato plants to 13 h of 0.8 W m^{-2} UV radiation, while Wargent
321 et al. (2015) used 10 kJ m^{-2} d^{-1} on lettuce. To be noted is that most experiments using higher UV
322 doses mimic sunlight and provide UV radiation during the light period. Background PAR intensity
323 has been shown to affect plant injury by UV radiation, therefore night time UV doses should be
324 low so as to avoid UV induced injury. Plant responses to UV radiation are dose dependent, with
325 two seemingly separate, though interacting, regulatory pathways inducing morphogenic and stress-
326 related responses Robson et al. (2015). Despite much research done on the effects of UV radiation
327 on plants, there remains great uncertainty regarding the UV-B dose underpinning plant
328 morphogenesis. Additionally, UV dose alone does not determine plant responses, as response to
329 UV is modulated by other climate factors, which may influence both magnitude and direction of
330 response (Robson et al., 2015). Background PAR level has been shown to be an important factor
331 in this environmental filter (Cen & Bornman 1990; Lydon et al. 1986; Meijkamp et al. 2001;
332 Wargent et al. 2009), and the ratio of UV-B/PAR is a determining factor in the plant's UV response
333 (Deckmyn et al. 1994). Plants exposed to higher background PAR were shown to be less
334 susceptible to UV-B-induced damage (Cen & Bornman 1990; Deckmyn et al. 1994), due to a
335 greater accumulation of protective pigments in the leaves. In this experiment, no visible injuries
336 were observed in vegetative 'CF' plants exposed to UV radiation.

337 Leaf damage in the form of bronzed patches was, however, seen in generative 'IR' and 'BBR'
338 plants exposed to the same UV dose as vegetative 'CF'. Similarly, Deckmyn and Impens (1998)
339 found generative growth to be more sensitive to UV-B radiation than vegetative growth in *Bromus*
340 *catharticus* grown at three solar UV levels. Damage in this experiment may have occurred due to

low production of protective pigments or photolyase, a light-dependent enzyme which repairs UV-induced DNA damage through photoreactivation (Strid et al. 1994). Photoreactivation is driven by both UV-A radiation and blue (B) light, and while the UV lamps provide some UV-A radiation, the supplementary light from the HPS lamps used in this experiment contains ~5% B light (Arve et al. 2015). Furthermore, in the experiment with generative plants, UV radiation was given at the end of the light period, when there is little B light to drive photoreactivation, which may have increased the generative plants' susceptibility to damage. Furthermore, vegetative 'CF' plants were exposed to 20 h light daily and thus a higher total DLI than generative plants (10 h daily). It is postulated that the UV-B/PAR ratio over time (e.g. per day) may affect plant resistance to UV-induced damage through the accumulation of protective pigments, though this has not been investigated.

4.2. UV exposure in moderate RH results in more compact poinsettia

The two generative cultivars investigated here showed similar responses to UV when grown in moderate RH but not in high RH (Tables 3 and 4). The responses to UV in moderate RH included typical UV induced responses such as decreases in plant diameter, leaf and bract area, and bract thickness, as well as increases in leaf thickness and chlorophyll content and reduced plant biomass. In plants grown in high RH there were some differences in response between the two cultivars even though they were grown in the same growth chamber. Differences in intraspecific UV responses are common and have previously been found in both soybean and cowpea (Baroniya et al. 2011; Surabhi et al. 2009).

Reduced plant and leaf biomass are commonly reported responses to UV radiation (Cen & Bornman 1990; Nogués et al. 1998; Surabhi et al. 2009; Teramura et al. 1991), though both

Teramura et al. (1991) and Surabhi et al. (2009) found this decrease to be only in UV-sensitive cultivars of rice and cowpea, while UV-tolerant cultivars showed an increase in shoot DM in response to UV. While no differences in biomass were seen in vegetative plants, a trend towards reduction in biomass was seen in moderate RH compared to high RH in generative plants (Figure 2). Both generative cultivars showed significantly reduced biomass with UV exposure in moderate RH. Only 'IR' plants showed a significant reduction in biomass with UV exposure in high RH. The results described in this study allow us to conclude that plant responses to UV are dependent on the aerial environment and that poinsettia respond more strongly to UV in moderate RH compared to high RH.

While both 'IR' and 'BBR' plants grown in high RH showed a significant reduction in leaf area when exposed to UV similar to that of plants produced in moderate RH, both cultivars showed a significant increase in bract area, contradictory to the reduction in bract area seen after UV exposure in moderate RH (Table 4). Reduced leaf area is a commonly reported response to UV exposure (Cen & Bornman 1990; Meijkamp et al. 2001; Nogués et al. 1998), and has been attributed to the inhibition of epidermal cell division (Wargent et al. 2009), the inhibition of adaxial pavement cell expansion (Hectors et al. 2010), or a combination of these processes (Robson et al. 2015), though this was not investigated in this study. The reason for the UV induced increase in bract area in high RH is not known but might reflect a different hormonal or metabolic state of these plants as mentioned above.

High RH, experienced by the plant as a low vapour pressure deficit (VPD) is known to change plant metabolism and reduce stomatal function compared to plants grown in moderate RH (Arve et al. 2013; Lihavainen et al. 2016). In both generative cultures there was a trend towards decreased leaf conductance upon exposure to UV in plants grown in moderate RH, yet conductance increased

387 in UV-exposed plants grown in high RH (Table 5). The content of hormones such as abscisic acid
388 (ABA) is reported to be reduced in plants produced in high RH due to inactivation of ABA (Arve
389 et al. 2013; Okamoto et al. 2009). ABA and its metabolites were not measured in this study, but
390 the increased leaf and bract conductance seen in both generative cultivars produced in high RH
391 compared to moderate RH (Table 5) might indicate a reduced ABA content. It has been discussed
392 by others that the response to UV might be dependent on the presence of ABA in the plant tissue.
393 For instance, Tossi et al. (2009) showed that ABA was required for nitric oxide (NO) production
394 and responses to UV in UV-B-irradiated maize (*Zea mays*) seedlings. NO production is an
395 important signal involved in stomatal closure of plants and stem extension growth (Tossi et al.
396 2014).
397
398 ***4.3. Evaluation of UV as a tool to control morphology and practical implications***
399 Increasing the amount of B light (Britz & Sager 1990; Brown et al. 1995; Mortensen & Fjeld
400 1998) or increasing the red (R)/far red (FR) light ratio through the use of FR-screening filters
401 (Rajapakse & Kelly 1992; Rajapakse et al. 1999) have been shown to be effective means of using
402 the light environment to control plant height, indicating an average plant height reduction of 25%
403 in the abovementioned studies. UV-B alone has been shown to reduce plant height, but not as
404 effectively as the other light treatments (e.g. Nogues et al., 1998), and we found no reductive effect
405 on plant height in our experiments. There was, however, a reduction in plant diameter in moderate
406 RH in all cultivars in response to UV radiation. Thus, the UV treatment given in our experiments
407 was not strong enough to combat the morphological impacts of growth in high RH. However, in
408 *Pisum sativum*, UV exposure combined with a six-hour temperature drop in the middle of the light
409 period resulted in a 40% reduction in shoot elongation compared to non-UV-exposed plants (Roro

2015). This and further instances of interactions between UV radiation and growth conditions (Meijkamp et al. 2001; Roro 2015) indicates a potential for UV radiation, in combination with the right growth conditions, and with specific focus on damage avoidance, to be efficient as a means of plant morphological control. In addition to the effect of UV radiation on plant height, UV has also been shown to induce plant responses which may be beneficial in commercial production. For example: Martínez et al. (2004) found that exposure to stressful UV-C radiation accelerated flowering in *Arabidopsis thaliana* and Tossi et al. (2014) reported reduced stomatal conductance after UV-B exposure, while several authors have reported increased resistance to *Botrytis cinerea* with both UV-B (Demkura & Ballaré 2012; Marquenie et al. 2003) and UV-C (Mercier et al. 1993) treatment. In this study with poinsettia as a model, UV treatment did not affect photosynthesis, flowering time, leaf or bract conductance and could not repress the increased transpiration commonly seen in plants produced in high RH. However, under optimised growth conditions, UV radiation may be a beneficial means of controlling plant diameter and compactness of poinsettia and may reduce disease severity simultaneously.

5. Conclusion

The results presented here indicate that both the magnitude and direction of plant responses to UV are, to some extent, driven by the humidity in which the plants are grown. Poinsettia plants exposed to UV showed more compact lateral growth in a background of moderate RH but not in high RH. Plant height was increased in high humidity and exposure to UV radiation did not reduce this, as was hypothesised. Hence, factors such as RH should be taken into account when designing both experiments and production systems with UV radiation as a tool.

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7. References

Alem, P., Thomas, P. A. & van Iersel, M. W. (2015). Controlled Water Deficit as an Alternative to Plant Growth Retardants for Regulation of Poinsettia Stem Elongation. *HortScience*, 50 (4): 565-569.

Arve, L. E., Terfa, M. T., Gislerød, 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): 382-392.

Arve, L. E., Terfa, M. T., Suthaparan, A., Poudel, M. S., Gislerød, H. R., Olsen, J. E. & Torre, S. (2015). *Aerial environment and light quality during production affect postharvest transpiration of ornamentals*: International Society for Horticultural Science (ISHS), Leuven, Belgium. 197-204 pp.

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.

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.

456 Brown, C. S., Schuerger, A. C. & Sager, J. C. (1995). Growth and photomorphogenesis of pepper
457 plants under red light-emitting diodes with supplemental blue or far-red lighting. *Journal*
458 *of the American Society for Horticultural Science*, 120 (5): 808-813.
459 Cen, Y.-P. & Bornman, J. F. (1990). The response of bean plants to UV-B radiation under different
460 irradiances of background visible light. *Journal of Experimental Botany*, 41 (11): 1489-
461 1495.
462 Craver, J. K., Miller, C. T., Williams, K. A. & Bello, N. M. (2014). Ultraviolet radiation affects
463 intumescence development in ornamental sweetpotato (*Ipomoea batatas*). *HortScience*, 49
464 (10): 1277-1283.
465 De Castro, V. L., Goes, K. P. & Chiorato, S. H. (2004). Developmental toxicity potential of
466 paclobutrazol in the rat. *International Journal of Environmental Health Research*, 14 (5):
467 371-380.
468 Deckmyn, G., Martens, C. & Impens, I. (1994). The importance of the ratio UV-B/photosynthetic
469 active radiation (PAR) during leaf development as determining factor of plant sensitivity
470 to increased UV-B irradiance: effects on growth, gas exchange and pigmentation of bean
471 plants (*Phaseolus vulgaris* cv. Label). *Plant, Cell & Environment*, 17 (3): 295-301.
472 Deckmyn, G. & Impens, I. (1998). Effects of solar UV-B irradiation on vegetative and generative
473 growth of *Bromus catharticus*. *Environmental and Experimental Botany*, 40 (2): 179-185.
474 Demkura, P. V. & Ballaré, C. L. (2012). UVR8 mediates UV-B-induced *Arabidopsis* defense
475 responses against *Botrytis cinerea* by controlling sinapate accumulation. *Molecular Plant*,
476 5 (3): 642-652.
477 Frohnmeyer, H. & Staiger, D. (2003). Ultraviolet-B radiation-mediated responses in plants.
478 Balancing damage and protection. *Plant Physiology*, 133 (4): 1420-1428.

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

Green, A. E. S., Sawada, T. & Shettle, E. P. (1974). The middle ultraviolet reaching the ground. *Photochemistry and Photobiology*, 19 (4): 251-259.

He, J.-M., Xu, H., She, X.-P., Song, X.-G. & Zhao, W.-M. (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., Jacques, E., Prinsen, E., Guisez, Y., Verbelen, J.-P., Jansen, M. A. K. & Vissenberg, K. (2010). UV radiation reduces epidermal cell expansion in leaves of Arabidopsis thaliana. *Journal of Experimental Botany*, 61 (15): 4339-4349.

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.

Islam, M. A., Kuwar, G., Clarke, J. L., Blystad, D.-R., Gislerød, H. R., Olsen, J. E. & Torre, S. (2012). Artificial light from light emitting diodes (LEDs) with a high portion of blue light results in shorter poinsettias compared to high pressure sodium (HPS) lamps. *Scientia Horticulturae*, 147: 136-143.

Islam, M. A., Tarkowská, D., Clarke, J. L., Blystad, D.-R., Gislerød, H. R., Torre, S. & Olsen, J. E. (2014). Impact of end-of-day red and far-red light on plant morphology and hormone physiology of poinsettia. *Scientia Horticulturae*, 174: 77-86.

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.

501 Jeon, M.-W., Ali, M. B., Hahn, E.-J. & Paek, K.-Y. (2006). Photosynthetic pigments, morphology
502 and leaf gas exchange during ex vitro acclimatization of micropropagated CAM
503 *Doritaenopsis* plantlets under relative humidity and air temperature. *Environmental and*
504 *Experimental Botany*, 55 (1–2): 183-194.
505 Leuschner, C. (2002). Air humidity as an ecological factor for woodland herbs: Leaf water status,
506 nutrient uptake, leaf anatomy, and productivity of eight species grown at low or high vpd
507 levels. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 197 (4): 262-274.
508 Lihavainen, J., Ahonen, V., Keski-Saari, S., Kontunen-Soppela, S., Oksanen, E. & Keinanen, M.
509 (2016). Low vapour pressure deficit affects nitrogen nutrition and foliar metabolites in
510 silver birch. *Journal of Experimental Botany*, 67 (14): 4353-65.
511 Lydon, J., Teramura, A. H. & Summers, E. G. (1986). Effects of ultraviolet-B radiation on the
512 growth and productivity of field grown soybean. In Worrest, R. C. & Caldwell, M. M. (eds)
513 *Stratospheric Ozone Reduction, Solar Ultraviolet Radiation and Plant Life*, pp. 313-325.
514 Berlin, Heidelberg: Springer Berlin Heidelberg.
515 Mackerness, S. A.-H.-., Surplus, S. L., Jordan, B. R. & Thomas, B. (1998). Effects of
516 supplementary ultraviolet-B radiation on photosynthetic transcripts at different stages of
517 leaf development and light levels in pea (*Pisum sativum* L.): Role of active oxygen species
518 and antioxidant enzymes. *Photochemistry and Photobiology*, 68 (1): 88-96.
519 Marquenie, D., Geeraerd, A. H., Lammertyn, J., Soontjens, C., Van Impe, J. F., Michiels, C. W.
520 & Nicolaï, B. M. (2003). Combinations of pulsed white light and UV-C or mild heat
521 treatment to inactivate conidia of *Botrytis cinerea* and *Monilia fructigena*. *International*
522 *Journal of Food Microbiology*, 85 (1–2): 185-196.

523 Martínez, C., Pons, E., Prats, G. & León, J. (2004). Salicylic acid regulates flowering time and
524 links defence responses and reproductive development. *The Plant Journal*, 37 (2): 209-
525 217.
526 Meijkamp, B. B., Doodeman, G. & Rozema, J. (2001). The response of *Vicia faba* to enhanced
527 UV-B radiation under low and near ambient PAR levels. In Rozema, J., Manetas, Y. &
528 Björn, L.-O. (eds) *Responses of Plants to UV-B Radiation*, pp. 135-146. Dordrecht:
529 Springer Netherlands.
530 Mercier, J., Arul, J. & Julien, C. (1993). Effect of UV-C on phytoalexin accumulation and
531 resistance to *Botrytis cinerea* in stored carrots. *Journal of Phytopathology*, 139 (1): 17-25.
532 Mortensen, L. M. & Fjeld, T. (1998). Effects of air humidity, lighting period and lamp type on
533 growth and vase life of roses. *Scientia Horticulturae*, 73 (4): 229-237.
534 Mortensen, L. M. & Gislerød, H. R. (1999). Influence of air humidity and lighting period on
535 growth, vase life and water relations of 14 rose cultivars. *Scientia Horticulturae*, 82 (3–4):
536 289-298.
537 Mortensen, L. M. (2000). Effects of air humidity on growth, flowering, keeping quality and water
538 relations of four short-day greenhouse species. *Scientia Horticulturae*, 86 (4): 299-310.
539 Myster, J. & Moe, R. (1995). Effect of diurnal temperature alternations on plant morphology in
540 some greenhouse crops—a mini review. *Scientia Horticulturae*, 62 (4): 205-215.
541 Negash, L. & Björn, L. O. (1986). Stomatal closure by ultraviolet radiation. *Physiologia*
542 *Plantarum*, 66 (3): 360-364.
543 Nogués, S., Allen, D. J., Morison, J. I. L. & Baker, N. R. (1998). Ultraviolet-B radiation effects
544 on water relations, leaf development, and photosynthesis in droughted pea plants. *Plant*
545 *Physiology*, 117 (1): 173-181.

546 Nogués, S., Allen, D. J., Morison, J. I. L. & Baker, N. R. (1999). Characterization of stomatal
547 closure caused by ultraviolet-B radiation. *Plant Physiology*, 121 (2): 489-496.
548 Okamoto, M., Tanaka, Y., Abrams, S. R., Kamiya, Y., Seki, M. & Nambara, E. (2009). High
549 humidity induces abscisic acid 8′-hydroxylase in stomata and vasculature to regulate local
550 and systemic abscisic acid responses in *Arabidopsis*. *Plant Physiology*, 149 (2): 825-834.
551 Rajapakse, N. C. & Kelly, J. W. (1992). Regulation of chrysanthemum growth by spectral filters.
552 *Journal of the American Society for Horticultural Science*, 117 (3): 481-485.
553 Rajapakse, N. C., Young, R. E., McMahon, M. J. & Oi, R. (1999). Plant height control by
554 photoselective filters: Current status and future prospects. *HortTechnology*, 9 (4): 618-624.
555 Robson, T. M., Klem, K., Urban, O. & Jansen, M. A. K. (2015). Re-interpreting plant
556 morphological responses to UV-B radiation. *Plant, Cell & Environment*, 38 (5): 856-866.
557 Roro, A. G. (2015). *Impact of UV radiation on plant growth and development in different climatic*
558 *regimes*: Norwegian University of Life Sciences, Department of Plant Science.
559 Sørensen, M. T. & Danielsen, V. (2006). Effects of the plant growth regulator, chlormequat, on
560 mammalian fertility. *International Journal of Andrology*, 29 (1): 129-133.
561 Strid, Å., Chow, W. S. & Anderson, J. M. (1994). UV-B damage and protection at the molecular
562 level in plants. *Photosynthesis Research*, 39 (3): 475-489.
563 Surabhi, G.-K., Reddy, K. R. & Singh, S. K. (2009). Photosynthesis, fluorescence, shoot biomass
564 and seed weight responses of three cowpea (*Vigna unguiculata* (L.) Walp.) cultivars with
565 contrasting sensitivity to UV-B radiation. *Environmental and Experimental Botany*, 66 (2):
566 160-171.
567 Suthaparan, A., Stensvand, A., Solhaug, K. A., Torre, S., Mortensen, L. M., Gadoury, D. M., Seem,
568 R. C. & Gislerød, H. R. (2012). Suppression of powdery mildew (*Podosphaera pannosa*)

569 in greenhouse roses by brief exposure to supplemental UV-B radiation. *Plant Disease*, 96
570 (11): 1653-1660.
571 Suthaparan, A., Stensvand, A., Solhaug, K. A., Torre, S., Telfer, K. H., Ruud, A. K., Mortensen,
572 L. M., Gadoury, D. M., Seem, R. C. & Gislerød, H. R. (2014). Suppression of cucumber
573 powdery mildew by supplemental UV-B radiation in greenhouses can be augmented or
574 reduced by background radiation quality. *Plant Disease*, 98 (10): 1349-1357.
575 Teramura, A. H., Ziska, L. H. & Sztein, A. E. (1991). Changes in growth and photosynthetic
576 capacity of rice with increased UV-B radiation. *Physiologia Plantarum*, 83 (3): 373-380.
577 Torre, S. & Fjeld, T. (2001). Water loss and postharvest characteristics of cut roses grown at high
578 or moderate relative air humidity. *Scientia Horticulturae*, 89 (3): 217-226.
579 Torre, S., Fjeld, T., Gislerød, H. R. & Moe, R. (2003). Leaf anatomy and stomatal morphology of
580 greenhouse roses grown at moderate or high air humidity. *Journal of the American Society*
581 *for Horticultural Science*, 128 (4): 598-602.
582 Torre, S., Roro, A., Bengtsson, S., Mortensen, L., Solhaug, K., Gislerød, H. & Olsen, J. (2012).
583 Control of plant morphology by UV-B and UV-B-temperature interactions. *Acta*
584 *Horticulturae* (956): 207.
585 Tossi, V., Lamattina, L. & Cassia, R. (2009). An increase in the concentration of abscisic acid is
586 critical for nitric oxide-mediated plant adaptive responses to UV-B irradiation. *New*
587 *Phytologist*, 181 (4): 871-879.
588 Tossi, V. E., Lamattina, L., Jenkins, G. & Cassia, R. (2014). UV-B-induced stomatal closure in
589 *Arabidopsis* is regulated by the UVR8 photoreceptor in an NO-dependent mechanism.
590 *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): 315-326.

Wargent, J. J., Nelson, B. C. W., McGhie, T. K. & Barnes, P. W. (2015). Acclimation to UV-B radiation and visible light in Lactuca sativa involves up-regulation of photosynthetic performance and orchestration of metabolome-wide responses. *Plant, Cell & Environment*, 38 (5): 929-940.

Wargent, J. J. (2016). *UV LEDs in horticulture: from biology to application*. 8th International Symposium on Light in Horticulture, East Lansing, Michigan, USA: Acta Hort.

8. Table and Figure Captions

Table 1. Experimental growth chamber setup for experiments 1 and 2. / indicates experiment 1 and 2 respectively, where differences occurred. Chambers were set up in a factorial design, with plants grown in either moderate (60%) or high (90%) RH and either not exposed (-UV) or exposed (+UV) to 0.15 W m^{-2} UV radiation for 40 minutes per day (time of day differs between experiments).

Table 2. Effects of RH and UV radiation on morphological parameters of vegetative 'Christmas Feelings' 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} UV radiation (+UV) during the dark period or not (-UV).

Table 3. Effects of RH and UV radiation on morphological parameters associated with elongation of generative 'Infinity Red' and 'Bravo Bright Red' poinsettia (means ± SE, n = 10 for each treatment)

615 grown for 58 days under 10/14 h light/dark SD treatment. Plants were grown in growth chambers under
616 one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV
617 radiation (+UV) or not (-UV).
618
619 Table 4. Effects of RH and UV radiation on morphological parameters associated with leaves of
620 generative 'Infinity Red' and 'Bravo Bright Red' poinsettia (means ± SE, *n* = 10 for each treatment)
621 grown for 58 days under 10/14 h light/dark SD treatment. Plants were grown in growth chambers under
622 one of two levels of RH (60 % or 90 %) and either exposed for 40 minutes to 0.15 W m^{-2} EOD UV
623 radiation (+UV) or not (-UV).
624
625 Table 5. Effects of RH and UV radiation on leaf and bract conductance and leaf photosynthesis (means ±
626 SE, *n* = 10 for each treatment) of generative 'Infinity Red' and 'Bravo Bright Red' poinsettia grown for 58
627 days under 10/14 h light/dark SD treatment and measured under light conditions. Plants were grown in
628 growth chambers under 60 % or 90 % RH and either exposed to 0.15 W m^{-2} for 40 minutes EOD UV
629 radiation (+UV), or not (-UV). Photosynthesis measurements took place inside the growth chambers,
630 while plants were removed from the chambers and placed at 20°C and 45%RH for conductance
631 measurements (described in Arve et al., 2015).
632
633 Figure 1. Spectral power distribution (SPD) for Q-panel UV 313 lamps (Q-Lab Corporation, Ohio, USA)
634 measured in W m^{-2} nm^{-1}. Adapted from Q-Lab Corporation. UV-A, UV-B and UV-C regions are
635 indicated.
636
637 Figure 2. Distribution of dry biomass between leaves, bracts and stems (*n* = 10 for each treatment, *n* = 40
638 for each cultivar) for generative poinsettia 'Bravo Bright Red' and 'Infinity Red', grown for 58 days
639 under 10/14 h light/dark treatment. The plants were grown in growth chambers under 60 % or 90 % RH
640 and either exposed for 40 minutes daily to 0.15 W m^{-2} EOD UV radiation (+UV) or not (-UV). Percentage

biomass distribution is indicated for leaves, bracts and stems separately. Letters indicate significant differences in total biomass between treatments.

Table 1

	Temperature (°C)	RH (%)	PAR irradiance (µmol m^{-2} s^{-1})	UV radiation (W m^{-2})	UV duration, time of day	Absolute UV dose (W m^{-2} d^{-1})	Photoperiod (h)	Daily light integral (mol m^{-2} d^{-1})
Chamber 1 (60-UV)	21 / 22	60 %	150 ± 10	0	NA	NA	20h / 10h	10.8 / 5.4
Chamber 2 (60+UV)	21 / 22	60 %	150 ± 10	0.15	40 mins, Night	360	20h / 10h	10.8 / 5.4
Chamber 3 (90-UV)	21 / 22	90 %	150 ± 10	0	NA	NA	20h / 10h	10.8 / 5.4
Chamber 4 (90+UV)	21 / 22	90 %	150 ± 10	0.15	40 mins, EOD	360	20h / 10h	10.8 / 5.4

Table 2

	60% RH		**90% RH**		**Significance Level**		
	-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
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 ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 3

	60 % RH		90 % RH		Significance Level		
	-UV	+UV	-UV	+UV	RH	UV	RHxUV
'Infinity Red'							
Plant Height (cm)	16.50 ± 0.5	16.90 ± 0.31	16.85 ± 0.40	18.45 ± 0.43	*	*	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
'Bravo Bright Red'							
Plant Height (cm)	10.65 ± 0.41	10.10 ± 0.41	9.95 ± 0.35	10.20 ± 0.35	NS	NS	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

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 ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 4

	60 % RH		90 % RH		Significance Level		
	-UV	+UV	-UV	+UV	RH	UV	RHxUV
'Infinity Red'							
Plant Diameter (cm)	36.60 ± 0.59	30.97 ± 0.49	31.20 ± 0.63	35.97 ± 1.03	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
'Bravo Bright Red'							
Plant Diameter (cm)	33.97 ± 0.79	29.77 ± 0.89	27.80 ± 1.03	28.95 ± 1.10	***	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	***	***	▪

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 ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

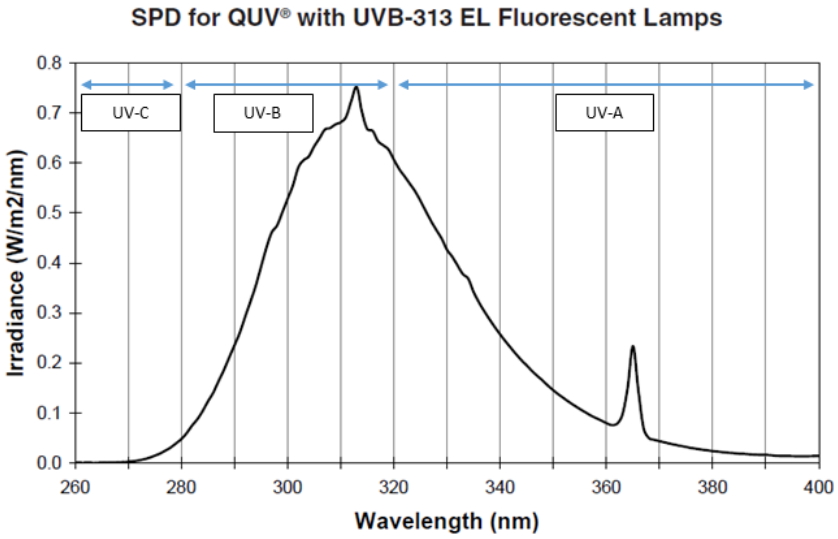
Table 5

	60 % RH		90 % RH		Significance Level		
	-UV	+UV	-UV	+UV	RH	UV	RH*UV
'Infinity Red'							
Leaf Conductance ($\mu mol\ m^{-2}\ s^{-1}$)	202.60 ± 18.61	198.70 ± 14.18	349.30 ± 16.74	363.60 ± 24.58	***	NS	NS
Bract Conductance ($\mu mol\ m^{-2}\ s^{-1}$)	21.64 ± 1.90	18.10 ± 1.94	23.80 ± 3.00	22.34 ± 1.54	NS	NS	NS
Photosynthesis ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	5.52 ± 0.17	5.20 ± 0.20	5.29 ± 0.18	5.23 ± 0.17	NS	NS	NS
'Bravo Bright Red'							
Leaf Conductance ($\mu mol\ m^{-2}\ s^{-1}$) ††	292.40 ± 16.87	254.10 ± 17.71	443.20 ± 60.14	522.00 ± 24.58	***	NS	NS
Bract Conductance ($\mu mol\ m^{-2}\ s^{-1}$)	22.08 ± 2.10	18.64 ± 2.41	32.90 ± 3.06	40.08 ± 1.54	***	NS	NS
Photosynthesis ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)	5.06 ± 0.11	5.06 ± 0.22	4.94 ± 0.20	5.27 ± 0.08	NS	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 ($p < 0.1$); ▪ $p < 0.1$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

684 Fig. 1



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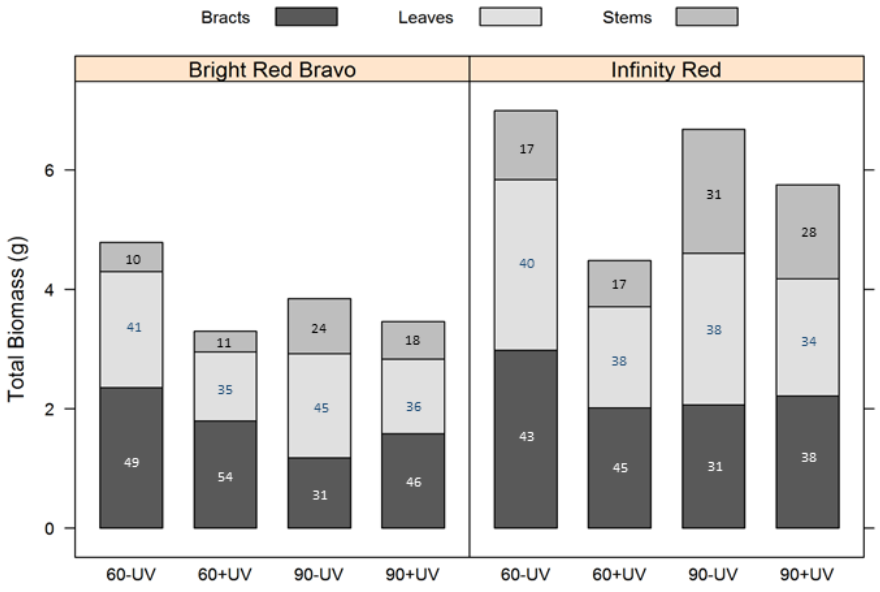
687 Fig. 2


Bracts
Leaves
Stems
Bright Red Bravo
Infinity Red
Total Biomass (g)
0
2
4
6
10
41
49
11
35
54
24
45
31
18
36
46
17
40
43
17
38
45
31
38
31
28
34
38
60-UV
60+UV
90-UV
90+UV
60-UV
60+UV
90-UV
90+UV

688