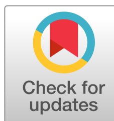

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Hormetic UV-C seed treatments for the control of tomato diseases

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Abstract

Hormesis is a dose response phenomenon in which low, non-damaging doses of a stressor bring about a positive response in the organism undergoing treatment. Evidence is provided here that hormetic UV-C treatments of tomato seed can control disease caused by *Botrytis cinerea, Fusarium oxysporum* f.sp. *lycopersici* (FOL) and f.sp. *radicis-lycopersici* (FORL) on tomato (*Solanum lycopersicum*). Treating seeds with a 4 kJ/m^2 dose of UV-C significantly reduced both the disease incidence and progression of *B. cinerea,* with approximately 10%

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reductions in both on the cv. Shirley. Disease severity assays for FOL and FORL on cv. Moneymaker showed dose-dependent responses: UV-C treatments of 4 and 6 kJ/m^2 significantly reduced the disease severity scores of FOL, whilst only the 6 kJ/m^2 showed significant reductions for FORL. To determine the effects of treatment on germination and seedling growth, UV-C doses of 4, 8 and 12 kJ/m^2 were performed on the cv. Shirley. No negative impacts on germination or seedling growth were observed for any of the treatments. The 8 kJ/m^2 treatment, however, showed significant biostimulation with increases in seedling, root and hypocotyl dry weight at 11.4, 23.1, and 12.0%, respectively, when compared to the control. Furthermore, significant increases in the root-mass fraction (10.6%) and root:shoot ratio (13.1%) along with a decrease in shoot-mass fraction (2.0%) indicates that the 8 kJ/m^2 treatment stimulated root growth to the greatest extent. There was no effect on hypocotyl and primary root length or the number of lateral roots indicating no adverse effects to basic root architecture or seedling growth.

Keywords: UV-C hormesis; *Solanum lycopersicum*; seed treatments; disease control; biostimulation

1 Introduction

Tomato is a globally important crop with a gross production value of $US 92,490 million globally in 2014 (FAO, 2018). Plant pathogens can cause devastating losses to tomato crops. For example, *Botrytis cinerea* and *Fusarium oxysporum* f.sp. *lycopersici* have been reported to cause crop losses of up to 70 and 80%, respectively (Borges *et al.,* 2014 & Nirmaladevi *et*

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al., 2016). With the introduction of EU legislation on the sustainable use of plant protection products and the emergence of fungicide resistance, limited disease control options are available to commercial producers. For instance, in the UK there is not a single approved fungicide against *Botrytis cinerea* for which resistance has not been observed on tomato (McPhearson, 2015). There is, therefore, an urgent need to identify effective alternatives to chemical control. Hormetic UV-C treatments may constitute one such alternative.

The portion of the electromagnetic spectrum between 100 and 280 nm is referred to as the UV-C region. Due to its germicidal action, high-dose UV-C treatments are used in the sterilisation of the surfaces of solids, liquids and gases. Such treatments, however, are not the focus of this study. UV-C hormesis is a phenomenon where low-dose, non-damaging UV-C exposures induce beneficial responses in the organism undergoing treatment. In 1987 the first observations of UV-C hormesis in fresh produce were published (Lu *et al.,* 1987). Hormetic UV-C treatments have now been shown to be effective on a wide range of fresh produce including both climacteric and non-climacteric fruit, tubers, salads and brassicas (Ranganna *et al.,* 1997; D'Hallewin *et al.,* 1999, Costa *et al.,* 2006; Pongprasert *et al.,* 2011 & Kasim & Kasim, 2012). The benefits of UV-C hormesis on fresh produce include disease resistance, delayed chlorophyll degradation and improved nutritional content; reviewed in depth by Shama & Alderson (2005), Ribeiro *et al.* (2012), Turtoi (2013) and Urban *et al.* (2016). More recently, UV-C treatments directed at seeds have shown to induce hormesis (Brown *et al.,* 2001). To date, however, only a small number of studies on the effects of UV-C seed treatment on disease resistance and plant physiology have been published. Two publications have reported that plants grown from UV-C-treated seed exhibit reduced levels

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of disease. Firstly, Brown *et al.* (2001) showed that a treatment of 3.6 kJ/m^2 reduced the incidence of *Xanthomonas campestris* pv. *campestris* by 75% on cabbage (*Brassica oleracea*). More recently, Siddiqui *et al.* (2011) reported reductions of up to 88% in the incidence of disease caused by *Fusarium* spp., *Rhizoctonia solani* and *Macrophomina phaseolina* on mung bean (*Vigna radiata*) and groundnut (*Arachis hypogaea*). The optimal UV-C dosage for disease resistance was shown to be dependent on the crop and pathogen undergoing investigation.

Further benefits of UV-C seed treatment include increased dry mass, increased germination rate, improved crop colour, delayed maturity, increased seedling vigour index and an increased number of root nodules (Brown *et al.,* 2001; Siddiqui *et al.,* 2011; Hamid & Javvaid 2011; Neelamegam & Sutha 2015). Additionally, lettuce (*Lactuca sativa*) and green bean (*Phaseolus vulgaris*) plants grown from UV-C-treated seed have shown an increased tolerance to salt stress (Aboul Fotouh *et al.,* 2014; Ouhibi *et al.,* 2014;).

The aim of this study was to explore the effect of a range of UV-C treatments on disease susceptibility to the necrotrophic tomato pathogens *Botrytis cinerea, Fusarium oxysporum* f.sp. *lycopersici* (FOL) and *radicis-lycopersici* (FORL). In addition, investigations into how UV-C seed treatment effects germination and seedling growth were conducted.

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2 Materials and methods

2.1 Seeds, seed storage and UV-C treatment

Seeds of the tomato cvs. Shirley and Moneymaker were purchased from Sow Seeds and Johnsons' Seeds, respectively. Seeds were stored at 6°C at a relative humidity of < 50%. UV-C treatments were performed with a U-shaped amalgam UV-C source (UVI 120 U 2G11 C P 15/469) with peak emission at 254 nm, obtained from Dr Hőnle AG, Gräfelfing, Germany. The source was housed within an anodised aluminium parabolic reflector. Seeds were treated at an intensity of 20 W m^{-2} and immediately stored in the dark at 21°C for 5 d following the procedures of Brown *et al.* (2001). UV-C intensity was measured using a radiometer (Model UVX, UVP Instruments) fitted with a 254 nm sensor.

2.2 Plant husbandry

Seeds were planted in 1 litre pots of Levington™ M3 compost and grown in a temperature controlled, ventilated glasshouse at the University of Nottingham. Lighting by the means of 400 W HPS SON-T lighting (Phillips) was used on a 16/8 h photoperiod. Day and night temperatures were 24/18 ± 2°C.

2.3 Pathogen maintenance, inoculum preparation and inoculation

Botrytis cinerea and FORL cultures were supplied from the University of Nottingham's fungal collection. The FOL culture was provided by Alison Jackson (The University of Warwick). Cultures were grown on potato dextrose agar (Sigma-Aldrich) supplemented with penicillin G sodium salt (Sigma-Aldrich) at 33 mg/L and streptomycin sulphate salt (Sigma-Aldrich) at

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133 mg/l. *Botrytis cinerea* cultures were grown in ambient light at room temperature and FOL and FORL cultures were kept in the dark at 27°C.

For *B. cinerea* inoculations, plants were grown under glass to the first signs of flowering (5 – 6 w). Prior to inoculation, plants were moved to a controlled environment using 400 W HPS SON-T lighting (Phillips) with a 16/8 h photoperiod at 21°C. Stem inoculations were then performed by removing a leaf and leaving a 10 mm petiole stub protruding from the stem; replicating a broken petiole. Petiole stubs were then inoculated with 10 µl of 5 x 10^6 spores/ml amended with 40% red grape juice. Calibrated spore solutions were prepared from 10 - 14 d old cultures following the procedures described by Scott *et al*. (2017). Three technical repeats were performed on each plant at true leaves 3, 4 and 5.

Stem lesion length was measured with Vernier callipers at 4 and 6 d post inoculation (DPI) and used to calculate the area underneath the disease progression curve (Equation 1).

$$\text{AUDPC} = \sum_{i=1}^{n} \frac{y_i + y_{i+1}}{2} (t_{i+1} - t_i)$$

Eq. 1. Area Underneath the Disease Progression Curve formula where *n*= total number of observations per inoculation point, *i*= observation, *y*= disease score and *t*= time (Jeger and Viljanen-Rollinson, 2001).

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FOL and FORL inoculations were performed on cv. Moneymaker seedlings 22 days after planting. A calibrated spore solution of 1 x 10^{6} spores per ml was made from 7 d old cultures. The compost was moistened, and seedlings were carefully removed. Roots were gently rubbed with Celite® (Sigma Aldrich) and incubated in 30 ml of spore solution for 2 h. Plants were re-potted and not watered until the following day. Disease severity was scored at 30 days post-inoculation following Reis & Boiteux (2007) and Parke & Grau (1993) for FOL and FORL, respectively. Two plants from each treatment group were mock inoculated and used as a control for the inoculation procedures.

2.4 Monitoring seed germination and seedling growth

Seedling germination and growth measurements were carried out according to the protocols of Ron *et al.* (2013). Following UV-C treatment, seeds were sterilised to prevent the growth of naturally occurring microflora. Seeds were washed in 70% ethanol for 2 min and 3% sodium hypochlorite (Sigma-Aldrich) for 20 min followed by 3 washes in sterile distilled water. Seeds were plated in a randomised block design on 120 mm square Petri dishes filled with 50 ml of Murashige and Skoog medium at 4.3 g/l (pH 5.8) amended with 0.8% agar technical No.3 (Oxoid); seven seeds were used per plate. Plates were sealed with surgical tape (3M) and stored vertically in a controlled environment with a 16 h photoperiod at 22°C. Germination was monitored for 7 d following plating.

Primary root and hypocotyl lengths were measured at 2 and 5 d post germination (DPG) with ImageJ. When individual seedlings reached 5 DPG they were dissected and dried for 24 h at 50°C to measure dry mass of the roots, hypocotyl and cotyledon. To measure

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germination, total germination percentage, germination index (Equation 2), T_{50} (Equation 3) and Z-index (Equation 4) were used. For measuring growth, root and stem mass fraction, root:shoot ratio and seedling vigour index II were calculated (Table 1).

$$GI = (7 \times n_1) + (6 \times \mathrm{n}_2) + \ \dots \ + \ (1 \times \mathrm{n}_7)$$

Eq. 2. Germination index (GI), where n_1, n_2, … , n_7 are the number of germinated seeds on the first, second and subsequent days until the 7th; 7, 6, … , 1 are the weights given to the seeds germinated on the first, second and 7th days, respectively (Walker-Simmons, 1987).

$$T_{50} = t_i + \frac{(N+1)/2 \ - \ n_i}{n_j - \ n_i} \ \times (t_j - \ t_i)$$

Eq. 3. The time to reach 50% germination (T_{50}) for the total number of seeds planted. *N* is the final number of seeds that have germinated, n_i and n_j are the total number of seeds germinated at adjacent time points t_i and t_j where $n_i < (N+1)/2 < n_j$ (Coolbear *et al.,* 1984).

$$Z = \sum \frac{Cn_{i,2}}{N} \quad where \ \ Cn_{i,2} = \frac{n_i(n_i - 1)}{2} \quad and \quad N = \frac{\sum n_i(n_i - 1)}{2}$$

Eq. 4. Synchrony of germination (Z-index) where n_i is the number of seeds germinated during the *i*th time (Ranal *et al.,* 2009).

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2.5 Experimental design and data analysis

For all experiments, data from each independent replicate experiment was combined prior to statistical analysis. For disease control experiments, UV-C doses of 2, 4 and 6 kJ/m^2 were applied alongside an untreated control. Three independent replicate experiments with a total of 24 biological and 72 technical repeats per treatment group were performed for experiments concerned with the control of *B. cinerea*. Due to inter-experimental variation in the susceptibility to *B. cinerea,* factor correction was performed following Ruijter *et al.* (2006). For the FOL and FORL disease control study, two independent experimental replicates were performed with a total of 12 biological repeats. A randomised experimental design was used in both *B. cinerea* and *F. oxysporum* studies. Data were analysed in SPSS (IBM) by Kruskal Wallis and Dunn's post-hoc test with Bonferroni correction.

For experiments in which the effect of UV-C seed treatment on germination and seedling growth were monitored, doses of 0, 4, 8 and 12 kJ/m^2 were applied. Three independent replicate experiments were performed, with a total of 63 biological repeats per treatment group. Data were analysed by one-way ANOVA with Tukey's post-hoc test. Where the homogeneity of variances assumption could not be met, Welch's robust ANOVA was performed followed by the Games-Howell post-hoc test. Statistical significance is defined as $p < 0.05$ for all experiments.

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3 Results

3.1 Disease control

For *B. cinerea* disease control assays, plants grown from seed treated with a dose 4 kJ/m^2 showed a statistically significant decrease in disease incidence when compared to the control and plants grown from seed treated with a 6 kJ/m^2 dose at 10.3% for both (Figure 1a). The 4 kJ/m^2 treatment also showed a significant reduction in the median disease progression (11.4%) in comparison to the control (Figure 1b).

Significant reductions in disease severity were observed for plants grown from UV-C-treated seed when inoculated with FOL or FORL (Figure 2). For FOL, both 4 kJ/m^2 and 6 kJ/m^2 doses significantly decreased disease severity with median scores dropping to 2.5 and 2.0 from 3.5 (control). A 6 kJ/m^2 dose significantly reduced FORL severity with a median of 1.5 compared to the control at 2.0 (Figure 2b). All mock inoculated plants were free from visible symptoms.

3.2 Effects on seedling growth

No significant differences in germination metrics were observed following treatment (Figure 3 and Table 2). Seeds treated with an 8 kJ/m^2 dose, however, showed slight reductions in the time to first germination event and time to 50% germination (T_{50}), while increases to the cumulative germination percentage, germination index, seedling vigour index-II and synchronicity of germination (Z-index) were observed when compared to the control (Table 2).

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At 5 DPG primary root and hypocotyl lengths were measured, seedlings were dissected, dried and weighed to determine the effect of treatment on the growth of major plant organs. Significant increases were observed for the total seedling, shoot, hypocotyl and root dry mass for the 8 kJ/m^2 treatment in comparison to the control with increases of 11.4%, 12.0%, 9.2% and 23.1%, respectively (Figure 4a, 4c, 4d and 4e). The cotyledon dry mass increased by 8% for the 8 kJ/m^2 treatment, in comparison to the control (Figure 4b). The difference, however, was not statistically significant.

No statistically significant differences in organ length were observed for any treatments (Figure 5). The number of lateral roots at was not affected by any of the treatments, although small increases were observed for the 4, 8 and 12 kJ/m^2 treatments (Figure 5d). Finally, a statistically significant increase in mean root-mass fraction (10.6%) and root:shoot ratio (13.1%) and a decrease in stem-mass fraction (2.0%) was observed for the 8 kJ/m^2 treatment in comparison to the control (Figure 6).

4 Discussion

Tomato seeds treated with UV-C doses of either 2, 4 or 6 kJ/m^2 were used to grow plants for disease control assays. *B. cinerea* inoculations were performed on broken petioles; a common site of natural inoculation in commercial glasshouses (Beyers *et al.,* 2014). Inoculations were performed during flowering as disease susceptibility increases during anthesis (Borges *et al.,* 2014). A 4 kJ/m^2 dose showed significant reductions in the incidence

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(10.3%) and progression (11.4%) of *B. cinerea*. Furthermore, our data indicates that disease control may have good longevity as plants were inoculated 5 to 6 weeks post planting.

Similar patterns in disease severity score were observed for FOL and FORL inoculations, with a reduction in high scoring plants as dose increased. FOL disease severity was significantly reduced with 4 and 6 kJ/m^2 treatments, while only the 6 kJ/m^2 treatment significantly reduced FORL disease severity.

These are the first observations of UV-C seed treatment disease control on tomato and indicate that UV-C seed treatments may provide versatile and residue-free disease control method. Furthermore, we have shown that UV-C seed treatments can successfully control different pathogens on contrasting cultivars at differing developmental stages.

Our findings are in accordance with Brown *et al.,* (2001) & Siddiqui *et al.,* (2011) who reported reduced incidence of *X. campestris* pv *campestris* on cabbage and *Fusarium* spp., *R. solani* and *M. phaseolina* on mung bean and groundnut following UV-C seed treatment. We have shown for the first time, however, that UV-C seed treatments can also reduce disease progression following a successful inoculation event.

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With high levels of fungicide resistance and a reduction in the number of authorised actives, UV-C seed treatment may provide a valuable addition to integrated disease management strategies. Commercial trials using naturally occurring disease, however, are required to determine the efficacy and the cost-benefit analysis of implementing UV-C seed treatments.

The mechanisms controlling UV-C seed treatment's disease control is unknown. Induced resistance, however, is a likely player and has been shown against *B. cinerea* following UV-C treatment of tomato fruit (Charles *et al*., 2008a & Scott *et al*., 2018). Resistance was underpinned by the constitutive upregulation of genes encoding pathogenesis related proteins (Glu-B, Chi-9 and P4) and increased concentration of phytoalexin rishitin (Charles *et al*., 2008a & Scott *et al.*, 2018). Gene priming may also play a role facilitating a rapid response to the first plant-pathogen interaction as a priming related expression profile was identified for PAL following inoculation (Scott *et al*., 2018).

To determine the effect of UV-C treatment on seedling growth, a 4 kJ/m^2 treatment was used alongside doses of 8 and 12 kJ/m^2 to ascertain whether higher doses of UV-C have detrimental effects on plant growth. No negative effects were observed on seedling germination, growth or basic root architecture for any treatment.

The 8 kJ/m^2 treatment, however, showed statistically significant biostimulation of seedling growth with an 11.4% increase in total seedling mass. Biostimulation of growth has also been observed by Brown *et al.,* (2001); Siddiqui *et al.,* (2011); Hamid & Javvaid, (2011) &

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Neelamegam & Sutha, (2015). Here, root mass was stimulated to the greatest extent (23.1%), while no differences in primary root length or lateral root number were observed. This may indicate an increase in root volume and a greater efficiency in nutrient and water acquisition, further investigations are required to establish this with certainty. Biostimulation of hypocotyl and shoot growth increased dry mass by 9.1% and 12.0%, respectively. No changes to hypocotyl length were observed. To elucidate the physiological changes underpinning biostimulation, future investigations should focus on organ-specific cellular volume, structure and organisation. Potential alterations to the cell wall such as lignin and suberin deposition should also be explored; as reported by Charles *et al.* (2008b) following UV-C treatment of tomato fruit.

Although significant increases in both root and shoot dry mass were observed for the 8 kJ/m^2 treatment, significant increases in root mass fraction and root:shoot ratio and a decrease in stem mass fraction were also observed (Figure 6c). This suggests that UV-C seed treatment induces systemic biostimulation that is weighted towards the roots; inferring either that photoassimilates are being directed favourably towards the root system or that it induces a perturbation in hormonal balance controlling plant development. This observation may be expected as environmental stresses have been shown to increase root:shoot ratio (Eghball and Maranville, 1993).

The 8 kJ/m^2 UV-C treatment may also lead to the biostimulation of germination as positive effects were observed on total germination %, germination index, synchronicity (Z index), seedling vigour index (II) and T_{50}. Further investigation is required to determine whether

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these effects are significant. Increases in the total germination percentage of UV-C treated seed, however, have been reported by Siddiqui *et al.* (2011), Hamid & Javvaid (2011) and Neelamegam & Sutha (2015).

To conclude, this study has identified that UV-C seed treatments are an effective disease control method against both foliar and root pathogens of tomato. Specific UV-C doses are required to elicit biostimulation or disease control and for different pathogens on different cultivars. Further investigation into the potential changes to crop physiology from vegetative growth to anthesis, fruit development and yield is required to elucidate the full potential of UV-C treatment on tomato. In addition, research into the molecular mechanisms underpinning disease control and biostimulation should also be undertaken.

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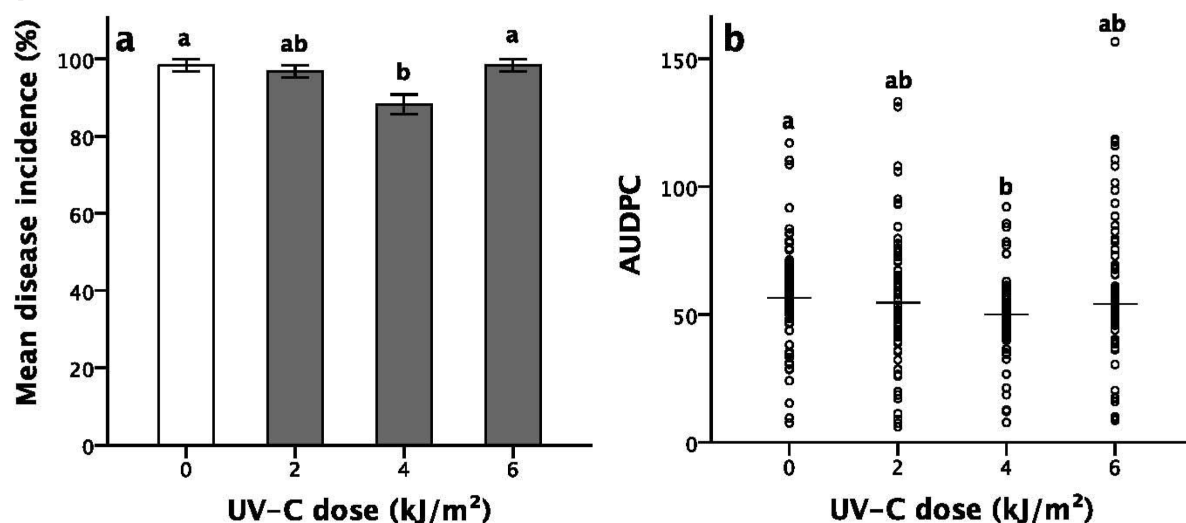
Table 1. Equations for growth metrics

Measure	Equation	Reference
Root mass fraction	Root mass ÷ total plant mass	Poorter & Ryser 2015
Stem mass fraction	Stem mass ÷ total plant mass	Poorter & Ryser 2015
Root:shoot ratio	Root mass ÷ Shoot mass	Monk, 1966
Seedling vigour index II	Germination percentage × mean dry weight	Kharb *et al.,* 1994

Table 2. Mean germination metrics of tomato seeds (cv. Shirley) following UV-C treatment

UV-C dose (kJ/m^2)	Total germination (%)	Germination index	T_{50}	Z-index	Seedling vigour index-II
0	93.65 ± 2.75	66.33 ± 10.97	4.23 ± 0.87	0.21 ± 0.04	335.87 ± 39.61
4	87.30 ± 7.27	63.33 ± 1.15	4.32 ± 0.08	0.21 ± 0.03	339.07 ± 80.40
8	95.24 ± 0.00	79.00 ± 3.00	3.41 ± 0.36	0.25 ± 0.05	386.51 ± 73.71
12	95. 24 ± 4.76	68.33 ± 4.04	4.13 ± 0.23	0.19 ± 0.01	377.39 ± 78.10

Means are accompanied by ± 1 S.E.M. N=63.



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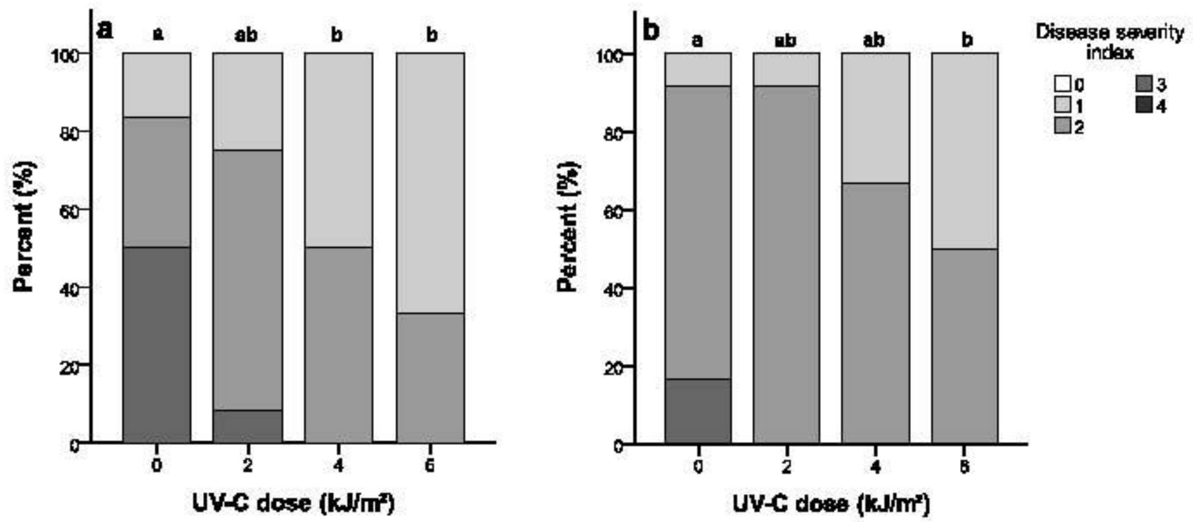

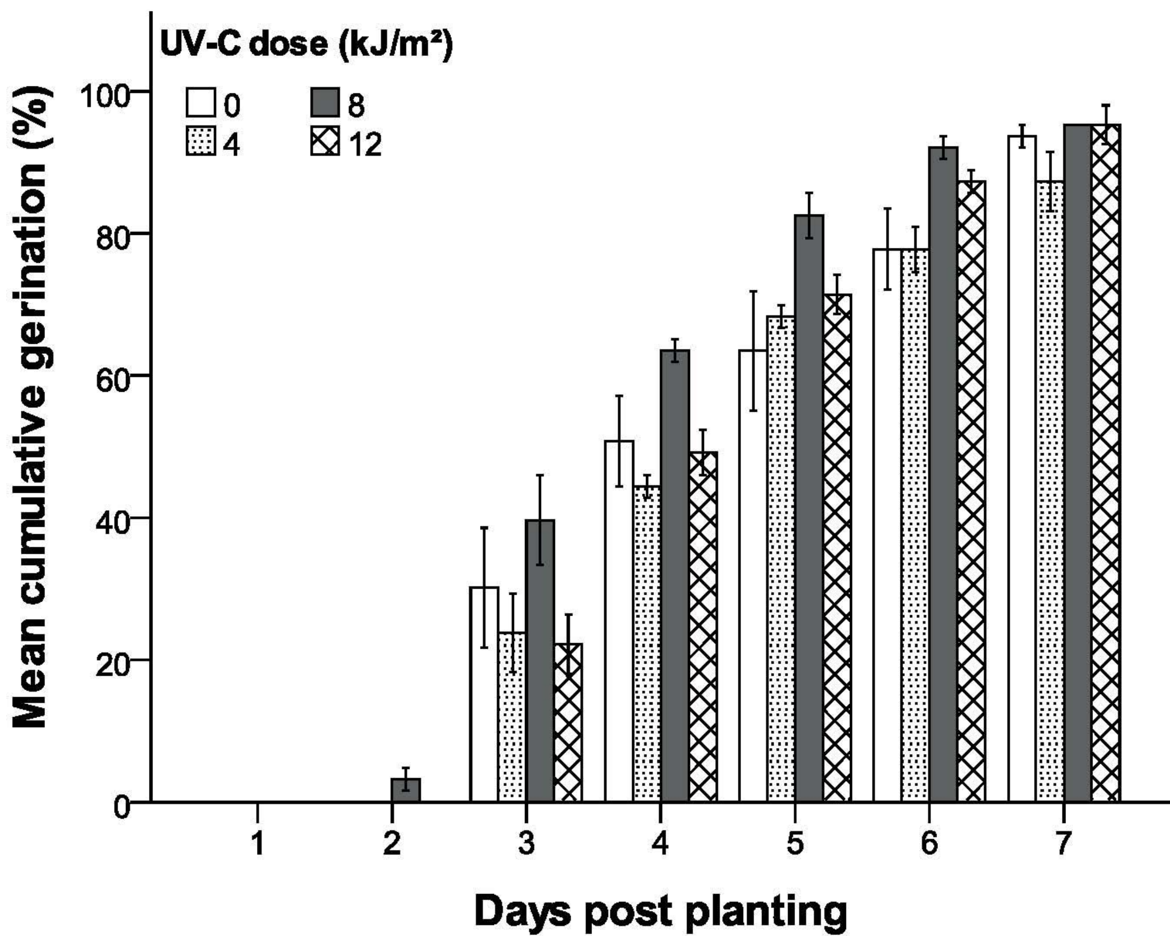

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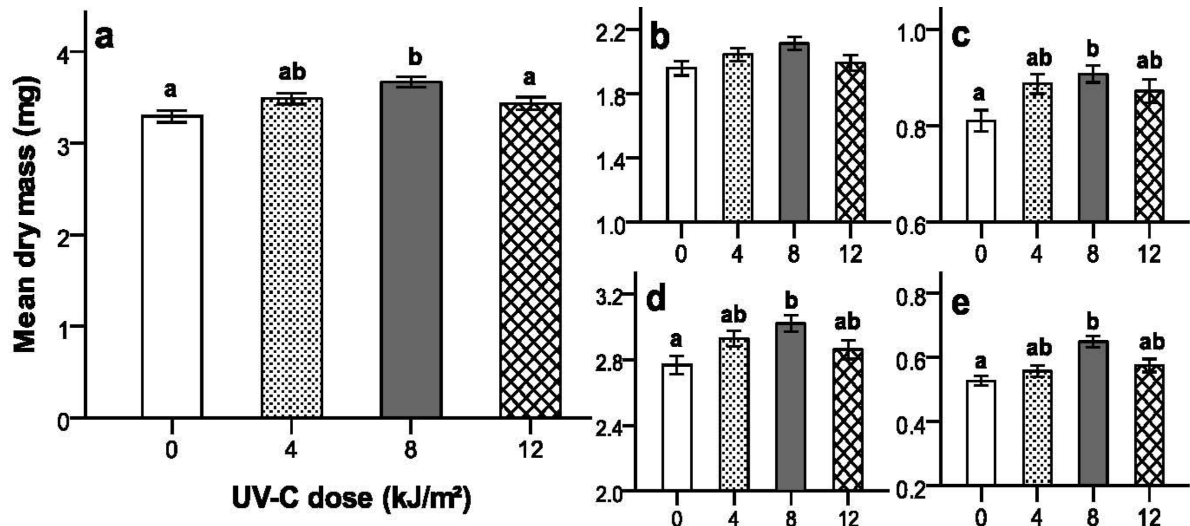

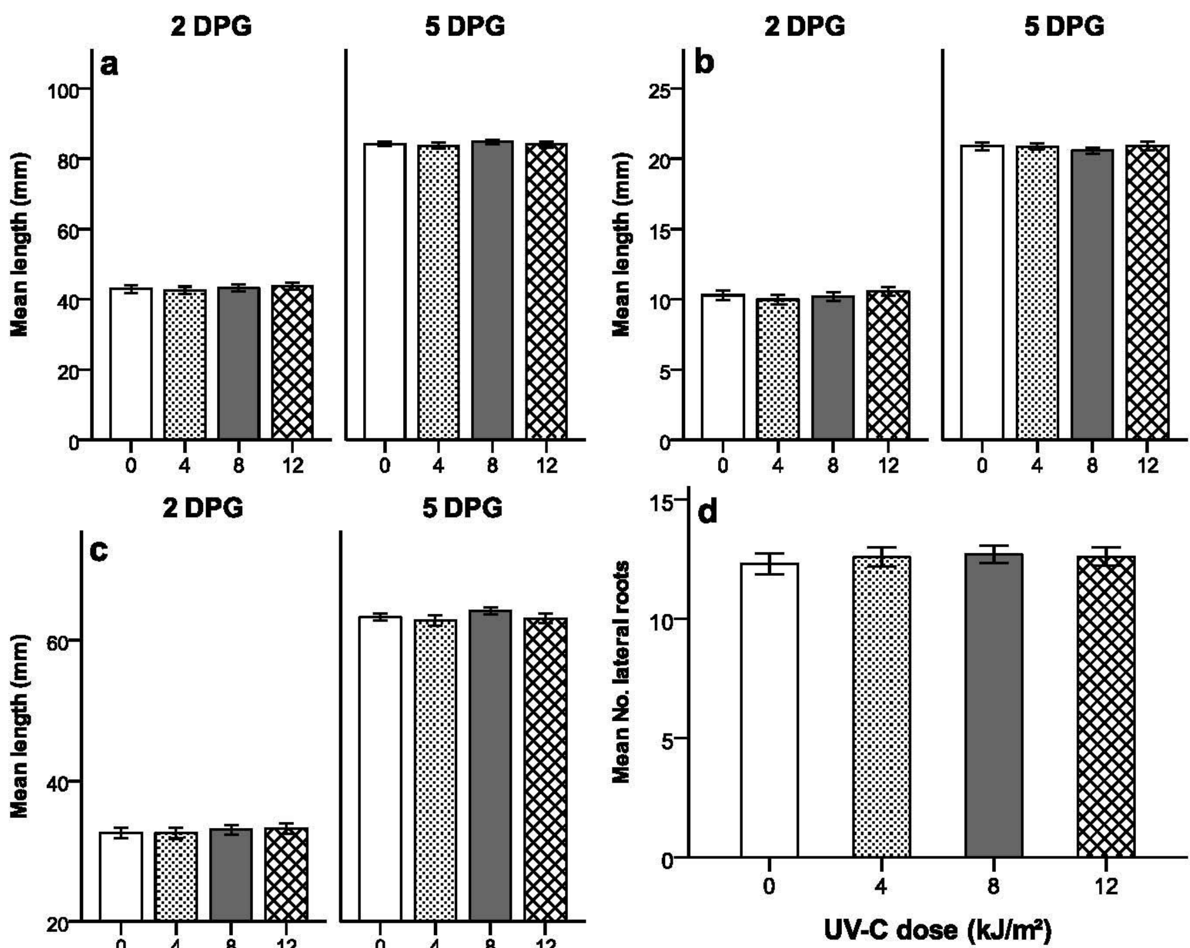

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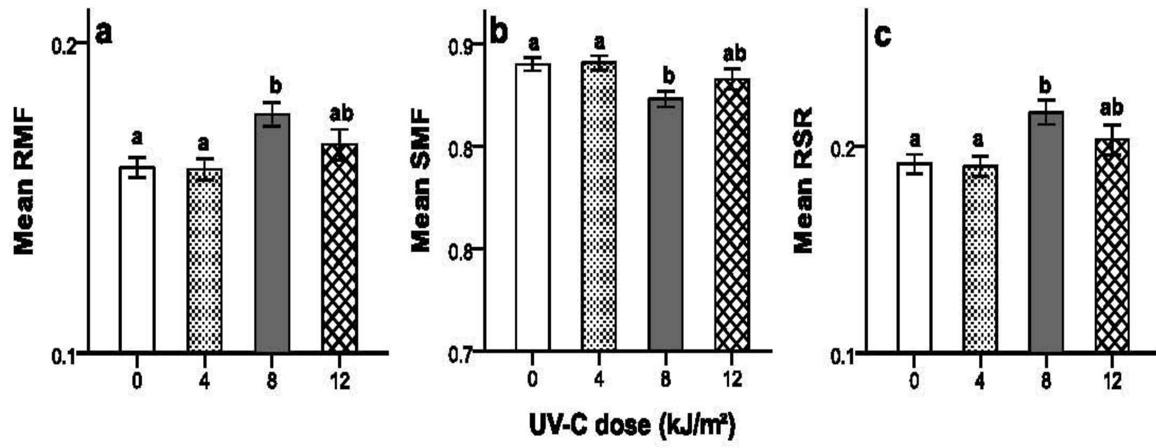

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