THESIS

# ULTRAVIOLET-B RADIATION EFFECTS ON SWEETPOTATO GROWTH AND DEVELOPMENT

Submitted by

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ABSTRACT

UTRAVIOLET-B RADIATION EFFECTS ON SWEETPOTATO GROWTH AND DEVELOPMENT

In spite of the success of the implementation of Montreal Protocol, the ozone level is not expected to return to 1980's levels until this mid-century because of the remaining chloroflurocarbon (CFCS) in the atmosphere. Therefore, ground-level Ultraviolet-B will still stay in a high level in the next several decades and be a significant factor on the growth and development of all crops including sweetpotatoes. Two experiments were conducted using sunlit plant growth chambers and greenhouse facilities at Mississippi State, MS from July to November, 2016. In Experiment 1, the influence of three levels of UV-B (0, 5 and 10 kJ $m^{-2}$ $d^{-1}$) on growth, development, and yield of three contrasting cultivars, Beauregard, Hatteras and LA 1188, were studied. In Experiment 2, interactive effects of three levels of nitrogen (100, 60 and 20%) and two levels of UV-B (0 and 10 kJ $m^{-2}$ $d^{-1}$) on one cultivar, Beauregard, growth and development evaluated. In both the experiments, growth and developmental parameters including storage root yield and physiological parameters, were measured at the final harvest and during the experiment. Vine length, measured at – days of planting, were shorter by 15 and 39% in Beauregard), and 1.4 and 18% in LA 1188 at ambient (5 kJ) and elevated (10 kJ) of UV-B, respectively. Similarly, total biomass was reduced by 62% (Beauregard) and 30% (Hatteras) due to the dysfunction of photosynthesis and total leaf area development. Moreover, in response to the ambient and projected UV-B, leaf thickness was reduced by 25-45% and 32-54% for three cultivars, respectively. Leaf wax and phenolic were increased in response to ambient and elevated UV-B in all cultivars. Based on the combined response index (CRI), Beauregard was classified as UV-B sensitive and Hatteras and LA 1188 were classified as UV-B tolerant. The greenhouse experiment showed that compared to

100% nitrogen (optimum) and 0 UV-B, 20% of nitrogen deficiency and projected UV-B reduced the longest vine length, the storage root dry weight and the total biomass by 29, 59 and 59%, respectively. Both elevated UV-B and nitrogen deficiency suppressed the sweetpotato growth, but the optimal nitrogen offset some of the damaging effects of UV-B. These results demonstrate that maintaining optimal nitrogen could reduce the damaging of UV-B on sweetpotato plants. Developing cultivars tolerant to UV-B will not only benefit in the current UV-B levels, but also in the projected UV-B radiation environments.

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# CHAPTER I: GENERAL INTRODUCTION

Because of the remaining ozone depletion substance in the atmosphere, the ground UV-B radiation will remain at high levels in the next several decades (Björn 2008; McKenzie 2011). UV-B radiation has significant damaging effects on DNA, protein and membrane of plants because they are UV-sensitive targets (Caldwell 1995, 1998; Jansen 1998). Approximately 20% of crops are sensitive to UV-B radiation including soybean (Koti 2007), cotton (Kakani 2003), and maize (Singh 2013; Wijewardana 2016).

Sweetpotato (Ipomoea batatas), as the seventh major food crop in the world (FAO, 2009), contributed more than $500 million to the U.S. economy in 2012 (USDA 2013). Previous studies showed that in general soil moisture, soil and air temperature, nitrogen fertilizer determined sweetpotato yield (Meyers 2014), but the UV-B effects on sweetpotato have not been studied. Moreover, UV-B effects usually depend upon on other stress factors, therefore the interactive effect of UV-B and these factors such as nutrients need to be investigated (Correia 2000). Two experiments were in Mississippi State University to study the UV-B effects on the three contrasting sweetpoatato cultivars' growth and yield, and to examine the interactive effect of nitrogen and UV-B radiation on sweetpotato growth and development.

# CHAPTER II: ULTRAVIOLET (UV)-B EFFECTS ON THE THREE CONTRASTING SWEETPOATATO CULTIVARS GROWTH AND YIELD

## INTRODUCTION

The solar Ultraviolet-B (UV-B) radiation at ground level is mainly influenced by ozone in the stratosphere because it is where most ozone resides in and absorbs approximately all the UV-C (200-280 nm), most of UV-B (280-315 nm) and a small amount of UV-A (315-400 nm) radiation. It was estimated that the peak value of UV-B might triple in the U.S in the next fifty years without Montreal Protocol (McKenzie 2011). However, in spite of the success of Montreal Protocol, the global averaged ozone level will not return to the 1980's level until the mid-century because of the remaining chlorofluorocarbons (CFCs) in the atmosphere (Björn 2008; McKenzie 2011). Besides ozone, ground-level UV-B is also determined by solar angles, cloud cover, aerosols/pollution, and surface albedo, which change with location and time.

Plants were significantly influenced by UV-B radiation (Wargent 2013). On the molecule level, UV-B radiation has damaging effects on the DNA, protein and membrane of plants because they are UV-sensitive targets (Jansen 1998; Björn 2008; Prado 2012). Approximately 20% of crops are sensitive to UV-B radiation in terms of total dry weight reduction (Teramura 1983). Previous studies had already covered soybean (Koti 2007), cotton (Kakani 2003), and mazie (Singh 2013; Wijewardana 2016). For example, it was found that 10 kJ m-2 d-1 UV-B, the projected UV-B level, had multiple negative effects on maize including reducing plant heights (by 36%), leaf areas (by 22%), and photosynthesis rates (by 5-15%) compared to 0 kJ m-2 d-1 treatment (Singh 2013). Similarly, soybean showed reduction in plant heights (by 7%), leaf areas (by 15%) and photosynthesis rates (by 26%) with the same UV-B treatments (Koti 2007). Besides these apparent impacts, the projected UV-B even altered the gene expression (Jansen 1998) and chemical composition in

leaves such as UV absorbing compounds and pigments. The maize experiment mentioned above also showed increase by 51% and 143% in phenolic concentration and wax content, respectively.

Sweetpotato (Ipomoea batatas), as one of the root crops, is usually cultivated in both high-temperature and rain-fed environments such as southern states and California (USDA 2002). The top four primary sweetpotato growing states, including Louisiana, Mississippi, California and North Carolina, account for 78% of U.S. sweetpotato production. The UV-B level in those states, for example CA, are as high as 7 kJ $m^{-2}$ $d^{-1}$ in 2015 (Figure 1).

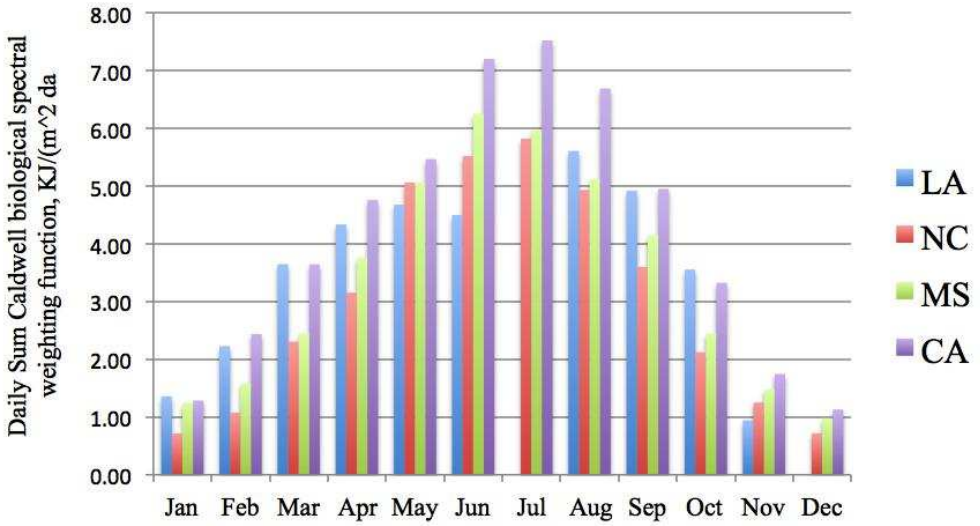


**Figure 1: Current (2015) UV-B levels (Average Daily –Sums Caldwell biological spectral weighting function, kJ $m^{-2}$ $d^{-1}$ in four U.S. States (LA: Louisiana; NC: North Carolina; MS: Mississippi; CA: California) that contribute most (>70%) sweetpotato production.**

Meanwhile, sweetpotato cultivars also have a strong adaptability to various environment conditions (Martin 1988). After it was introduced from Native South America 400 years ago, over 400 varieties of Sweetpotatoes are grown globally (Bailey 2017). Some of the commonly planted sweetpotato cultivars include Beauregard (BG), Hatteras (HT), and Louisiana 1188 (LA). Beauregard (BG), one of the most popular and well-studied cultivars released by LA agriculture experiment station in 1987, has a high-yield potential and strong resistance to soil rot/pox but weak resistance to root knot nematode (Wehner 2013). Hatteras (HT), released by North Carolina State University near 2011, received more research

attention than industry attention (Clark 2013). We know very few about the new variety, Louisiana 1188 (LA), and even less about their cultivars difference. In order to understand the variability among sweetpotato cultivars, we should not only focus on those high-yield ones such as Beauregard and Covington, but also the potential of those non-popular cultivars. Sweetpotato growth, especially the root initiation and development, in response to environmental factors induce significant alternation in yield and economic consequence (Godfray 2010). Previous studies showed that in general soil moisture, soil and air temperature, nitrogen fertilizers are such determinants (Meyers 2014). More specifically, the early-season soil moisture, temperature and nitrogen fertilizer determine root initiation; and the mid- and late-season ones determine biomass and yield (Villagarcia 1998; Ukom 2009; Gajanayake 2014, 2015, 2016).

Even though previous studies have already investigated the effects of those factors on the sweetpotato growth and yield, the UV-B effects on various sweetpotato cultivars have not been studied thoroughly. To understand the UV-B effects on sweetpotato growth and yield, one experiment was designed and conducted in the soil-plant-atmosphere research (SPAR) units where temperature, CO2 concentration, water content, and UV-B radiation were well controlled. Based on the current ground level monitoring and scenarios predicting future trend of UV-B radiation in Mississippi, three UV-B treatments (0, 5 and 10 kJ m-2 d-1) were imposed to simulate no UV-B, ambient UV-B and projected UV-B in Mississippi. The Photosynthesis rate, the stomatal conductance, the longest vine length, the leaf area, the total biomass, and other physiological parameters were measured and a combined response index was calculated. The objectives of this study were to quantify UV-B effects on the three contrasting sweetpoatato cultivars' growth and yield and to classify these three cultivars based on their sensitivity to UV-B radiation. We hypothesize that ambient and projected UV-B radiation of 5 and 10 kJ m-2 d-1 will have significant impacts on the sweetpotato growth

and yield, and cultivars sweetpotato (Beauregard, Hatteras, and Louisiana 1188) vary in their responses to current and projected UV-B radiation.

## MATERIALS AND METHODS

### Experimental facilities:

The soil-plant-atmosphere research (SPAR) units located at the Rodeney Foil Plant Science Research Center, Mississippi State, Mississippi, USA. The experiment was from July to October 2016. Each SPAR unit comprises of a steel soil bin, a Plexiglas chamber blocking the solar UV-B radiation, a system heating and cooling the air and a monitoring and control system. More details were described by Reddy and et al. (2001).

### Plant culture and cultivars:

Three cultivars of sweetpotato, Beauregard, Hatteras and LA 1188 were cut from field seedbeds, and within two days transplanted into white polyvinyl chloride (PVC) pots on 15 July, 2016. A total of 18 PVC pots (with 20 cm diameter and 30 cm height) were arranged randomly (9 rows, 6 pots per cultivar,) in each SPAR chamber. The pots were arranged with 26.6 cm row spacing and 25 cm apart within the row. The soil medium consisted of loam soil with a mix of 75% sand and 25% topsoil by volume with a 600 g of gravel at the bottom. Coarse gravel (600 g) were filled with a small hole at the bottom of each pot to allow extra water and nutrients solution to drain. A single slip with two nodes below the soil surface and two nodes above the soil surface was selected and transplanted into pot. Nodes above the soil surface contained two recently fully expanded leaves, while the nodes below the surface were clipped at base with 1-com in petiole length (Abukari 2015). Plants were grown under optimum water and nutrient conditions by irrigating each unit three times day using standard Hoagland's nutrient solution (Hewitt, 1951). The amount of irrigation in each unit was based on the evapotranspiration measured on the previous day (Reddy et al., 2001). During the experiment, to simulate natural shading effect caused by the surrounding edges of

sweetpotato canopy, variable black shade cloths were placed and adjusted twice weekly in each SPAR chamber.

**Treatments:**

The three UV-B treatments (0, 5 and 10 kJ $m^{-2}$ $d^{-1}$) were imposed at planting in all units and continued until the final harvest, 80 days after planting. A square-wave supplementation system composed of eight fluorescent lamps at a height of 0.5 meter above the canopy provided set UV-B levels in each treatment from 8:00 to 16:00 each day. These three treatments simulate no UV-B, ambient (5 kJ) and projected (10 kJ) of UV-B in the near future climate (Singh, 2014). Calcium diacetate films (CA) were wrapped around each lamp to filter UVC radiation and changed every 10-15 days, depending on the treatment level, to account degradation of the CA properties to treatment UV-B levels.. The UV-B radiation at the top of the canopy was monitored everyday using a UV-X digital radiometer and the dosage was adjusted using dimmable ballasts as needed.

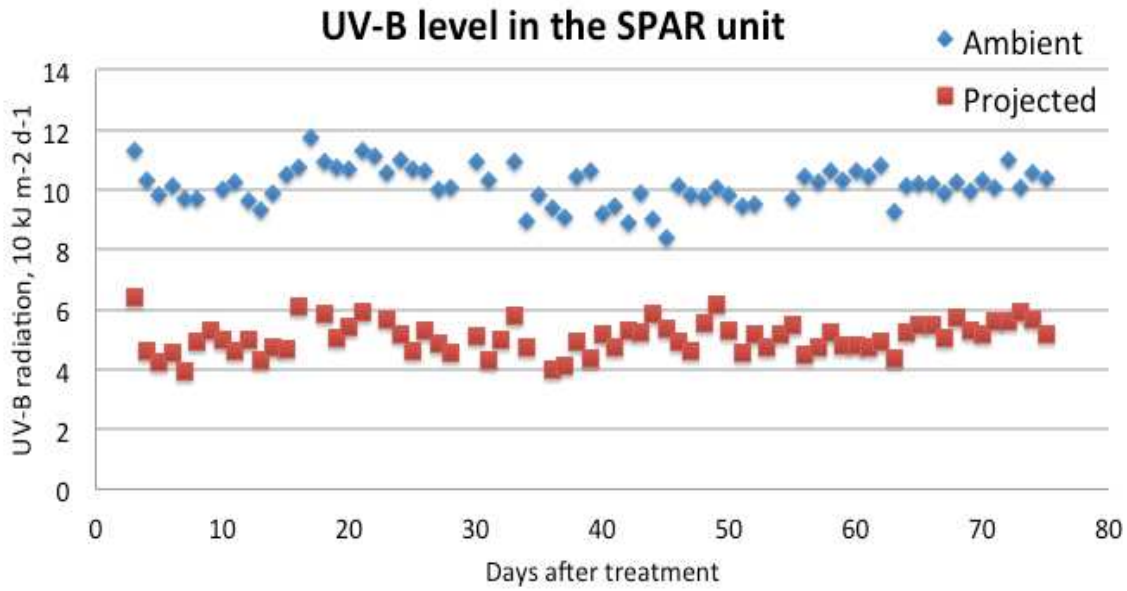


**Figure 2: Daily UV-B radiation level in the ambient and projected UV-B treatments monitored using a UVX digital radiometer at noon.**

**Photosynthesis and chlorophyll fluorescence measurements:**

On the uppermost third recently fully expended leaf, the photosynthesis (Pnet) and the value of the fluorescence in light (Fv′/Fm′) were measured under each of three UV-B treatments using an LI-6400 portable photosynthesis system (LiCOR Inc., Lincoln, NE, USA) three times at 34, 48 and 75 DAP through the experimental period. During the measurements, relative humidity was set to 50%; temperature was set to 30 $^{o}$C; $CO_2$ was set to 400 ppm; air flux was set to 400 µmol $s^{-1}$; saturation point was set 1500 µmol $m^{-2}$ $s^{-1}$. It often took four minutes to wait the total coefficient of variation (%CV) to reach a value below 0.5% before recording the parameters. The transpiration rate (Trmmol), stomatal conductance (Cond), Photosystem II (PhiPS2), and non-photochemical quenching (qN) were calculated by the LI-6400 instrument itself considering leaf area and incoming and outgoing flow rates.

**Leaf anatomical measurements:**

Recently, fully mature leaf samples from three plants were randomly selected from each cultivar in each treatment and segments of 2 cm long by 0.5 wide cut from 5 cm from

the base of the leaf blade and 2 –cm from the main midrib were stored in 2.5% glutaraldehyde in 0.1 M phosphate buffer for scanning electron microscope (SEM) analysis for surface wax structures. Then, another three specimens, collected in the same way, were fixed FAA (Farmaldehyde, acetic acid and alcohol at --- ratio by volume), and then processed for light microscopy. Sections of 10 micron thickness obtained as decribed in Kakani et al. (2003).Leaf thickness was determined based on those sections.

**Growth and developmental measurements:**

Longest vine length (LVL), longest vine node number (NN), storage root number (SRN) and total storage root fresh weight (TSRFW) were measured or counted on all plants at the final harvest, 80 DAP. Total leaf area (LA) was measured with the LI-3100 leaf area meter (Li-COR Inc., Lincoln, NE, USA) on all plants at the final harvest. Plant component dry weights, leaf weight (LW), stem weight (SW) and storage root weight (TSRDW) were measured by drying the material in a forced air oven that maintained at 80 C for 72 hours. Before drying the storage roots, storage roots were counted and fresh weight was recorded on all plants.

**Statistical analysis:**

Two-way ANOVA and LSD ($\alpha<0.05$) were used to determine the differences among UV-B treatments and cultivars using R-Studio. A linear regression model ($y=ax+b$) was used to estimate the relationship between UV-B and CRI using EXCEL.

**Combined response index (CRI) and UV-B sensitivity index (USI)**

Based on the index introduced by Dai et al. (1994) and later modified Koti et al. (2005, 2007), a combined response index (CRI) was calculated from the individual response indices calculated based on each parameter using the following formula.

$$CRI=[\frac{VLt-VLc}{VLc}+\frac{LAt-LAc}{LAc}+\frac{VNt-VNc}{VNc}+\frac{TBt-TBc}{TBc}+\frac{SRWt-SRWc}{SRWc}]*100$$

Where VL is the longest vine length, LA is the leaf area of the plant, VN is the node number of the longest vine, TB is the total biomass of the plant, and SRW is the total storage root dry weight of the plant under t (treatment) and c (control). The slope of regression curve of CRI against UV-B was calculated as a UV-B sensitivity index (USI). Based on the USI values, the cultivars were classified as tolerant and sensitive.

## RESULTS

### Photosynthesis and chlorophyll fluorescence

On 75 DAP, significant effects of UV-B ($P<0.01$) and cultivar ($P<0.05$) have been observed on the photosynthetic rate on the fifth fully expanded leaves (Table 1). Averaged over cultivar difference, UV-B significantly decreases P-net under projected UV-B by 16.6% compared to the control. Averaged over UV-B, photosynthetic rate (P-net) of BG (29.4 μmol $CO_2$ $m^{-2}$ $s^{-1}$) is significantly higher by 7.7% than LA (27.1 μmol $CO_2$ $m^{-2}$ $s^{-1}$). The maximum decline of P-net of BG and HT occurred at projected UV-B, and of LA at ambient UV-B treatment by 44, 10, 15%, respectively (Figure 3 A). Compared to the control, UV-B decreases stomatal conductance with maximum decline for BG at ambient and projected UV-B by 37 and 78%. UV-B also significantly affected fluorescence parameters such as Fv'/Fm' ($P<0.05$). (Table 1).

**Table 1: Effect of Ultraviolet-B radiation and cultivar Beauregard (BG), Hatteras (HT), Louisiana 1188 (LA) on photosynthesis (Pn), stomatal conductance (Cond), transpiration rate (Tr), water-use efficiency (WUE), PhiPS2 and Fv'/Fm' on the forth/fifth fully expended leaf at 75 DAP.**

| Cultivar | UV-B | Pn | Cond | Tr | WUE | PhiPS2 | Fv'/Fm' |
|---|---|---|---|---|---|---|---|
| | kJ m-2 d-1 | µmol CO2 m-2 s-1 | mol H2O m-2 s-1 | mmol H2O m-2 s-1 | µmol CO2 m-2 s-1 | | |
| BG | 0 | 35.17 | 0.65 | 9.85 | 3.93 | 0.26467 | 0.56322 |
| | 5 | 33.45 | 0.41 | 10.47 | 3.34 | 0.307 | 0.58537 |
| | 10 | 19.55 | 0.14 | 7.59 | 2.55 | 0.117 | 0.48437 |
| | ANOVA | ** | ns | ns | ns | ns | * |
| HT | 0 | 26.77 | 0.44 | 8.86 | 3.3 | 0.217 | 0.46 |
| | 5 | 30.77 | 0.34 | 9.47 | 3.32 | 0.27833 | 0.52 |
| | 10 | 24.17 | 0.35 | 7.8 | 3.22 | 0.163 | 0.46 |
| | ANOVA | ns | ns | ns | ns | ns | ns |
| LA | 0 | 27.40 | 0.42 | 8.71 | 3.17 | 0.26567 | 0.49 |
| | 5 | 23.20 | 0.26 | 8.1 | 2.92 | 0.18467 | 0.45 |
| | 10 | 30.80 | 0.51 | 9.55 | 3.2 | 0.2195 | 0.48 |
| | ANOVA | ns | ns | ns | ns | ns | ns |
| ANOVA | UV-B | ** | ns | ns | ns | ns | * |
| | Cultivar | * | ns | ns | ns | ns | ns |
| | UV-B x Cultivar | ** | ns | ns | ns | ns | ns |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''

**Table 2: Effect of Ultraviolet-B radiation and cultivar Beauregard (BG), Hatteras (HT), Louisiana 1188 (LA) on total leaf thickness and thickness of other component layers (palisade, mesophyll, upper and lower epidermis).**

| Cultivar | UV-B | Palisade | Mesophyll | Upper epidermis | Lower epidermis | Total leaf thickness |
|---|---|---|---|---|---|---|
| | kJ m-2 d-1 | µm per leaf | µm per leaf | µm per leaf | µm per leaf | µm per leaf |
| BG | 0 | 1116.54 | 888.7 | 315.78 | 372.08 | 2693.1 |
| | 5 | 921.92 | 684.54 | 196.44 | 208.04 | 2010.94 |
| | 10 | 642 | 711.36 | 239.74 | 228.52 | 1821.62 |
| | ANOVA | *** | *** | *** | *** | *** |
| HT | 0 | 826.28 | 540.4 | 209.64 | 220.36 | 1796.68 |
| | 5 | 980.1 | 876.42 | 196.26 | 208.88 | 2261.66 |
| | 10 | 813.9 | 665.68 | 197.62 | 199.26 | 1876.68 |
| | ANOVA | *** | *** | *** | *** | *** |
| LA | 0 | 608.74 | 487.6 | 182.76 | 206.06 | 1485.16 |
| | 5 | 836.42 | 892.6 | 205.86 | 211.26 | 2146.14 |
| | 10 | 1062.12 | 886.66 | 103.62 | 229.28 | 2281.68 |
| | ANOVA | *** | *** | *** | *** | *** |
| ANOVA | UV-B | *** | *** | *** | *** | *** |
| | Cultivar | *** | *** | *** | *** | *** |
| | UV-B x Cultivar | *** | *** | *** | *** | *** |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''

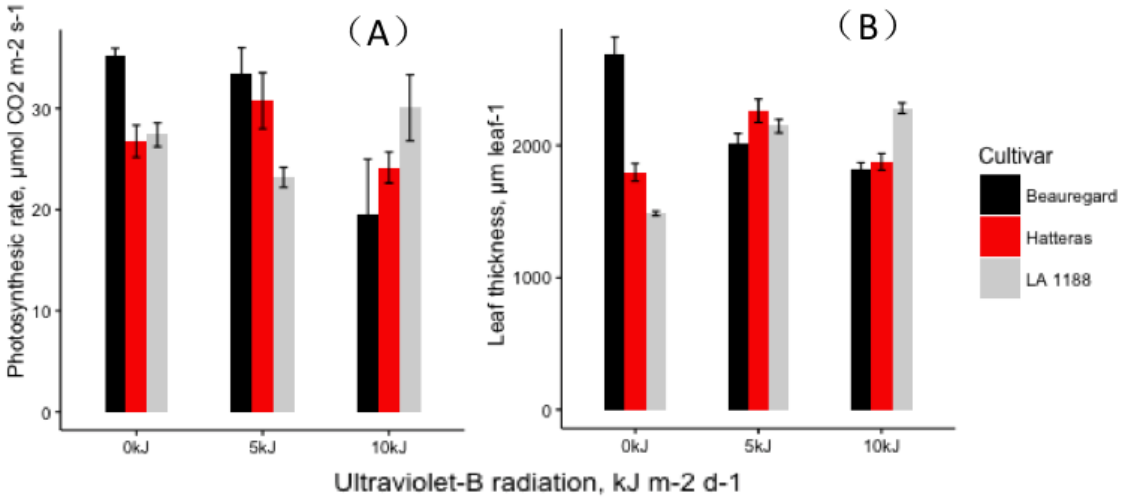


**Figure 3: Effect of Ultraviolet-B radiation (0, 5, 10 kJ $m^{-2}$ $d^{-1}$ UV-B) on (A) photosynthesis, $CO_2$ $m^{-2}$ $s^{-1}$ at 75DAP and (B) leaf thickness, µm per leaf of three cultivars (Beauregard, Hatteras, LA 1188). Bars in indicate standard errors of the three and ten replications for photosynthesis and leaf thickness, respectively.**

**Leaf structure**

Significant effects (P<0.001) of UV-B, cultivar and UV-B x cultivar interaction have been found on leaf thickness and all rest of internal component layers of leaf (palisade, mesophyll, upper and lower epidermis) (Table 2). UV-B significantly decreases total leaf thickness with maximum decline for BG at projected UV-B. However, UV-B also significantly increases total leaf thickness with maximum growth for HT at 5 kJ $m^{-2}$ $d^{-1}$, and for LA at 10 kJ $m^{-2}$ $d^{-1}$, respectively. Total leaf thickness of sweetpotato grown under control group is 2693µm (BG), 1797µm (HT) and 1485µm (LA). Compared to the control group, ambient and projected UV-B treatment decreases total leaf thickness by 25 and 32% for BG, and increases by 26 and 4% for HT, and 45% and 54% for LA, respectively (Figure 3 B).

**Epidermal ultrastructure observation**

Image filmed by SEM on adaxial surface demonstrated that over the cultivar difference, epidermal wax content reaches the maximum density at the ambient UV-B and minimum density at the projected UV-B (Figure 4).

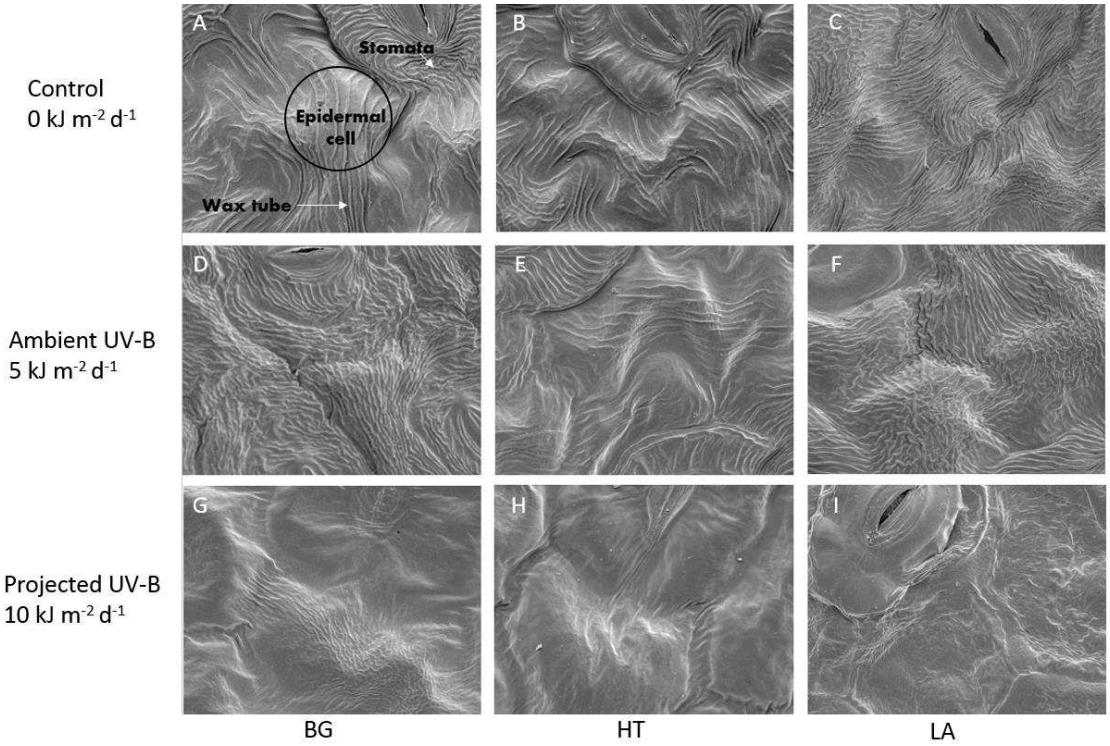


**Figure 4: Epicuticular wax morphology on leaf surfaces of sweet-potato exposed to control (A, B, C), ambient UV-B (D, E, F) and high UV-B (G, H, I) treatment. The figure shows that all three cultivars had a significant change on leaf surface morphology. For all three cultivars Beauregard (A, D, G), Hatteras (B, E, H) and Louisiana (C, F, I), all the wax tube intensity increased in the ambient UV-B and the epidermal cell suffered a critical damage in the high UV-B treatment. The size of guard cells and density of stomata also changed in the image.**

## Growth and yield

UV-B radiation had a significant effect on longest vine length ($P<0.05$), and the longest vine length also significantly varied among cultivars ($P<0.05$) (Table 3). UV-B significantly decreases longest vine length with maximum decline for BG and LA at projected UV-B (10 kJ $m^{-2}$ $d^{-1}$). Longest vine length of sweetpotato grown under control group (0 kJ $m^{-2}$ $d^{-1}$ UV-B) is 463.67 cm (BG) and 320.33 cm (LA). Compared to the control group, UV-B treatment of ambient (5) and projected (10 kJ $m^{-2}$ $d^{-1}$) UV-B decreases vine length by 15 and 39% for BG and 1.4 and 18% for LA, respectively (Figure 5 A). Cultivar HT shows an opposite trend that the vine length under projected UV-B increase 16% compared to control group.

**Table 3: Effect of Ultraviolet-B radiation and cultivar Beauregard (BG), Hatteras (HT), Louisiana 1188 (LA) on VL: vine length (cm), VNN: vine node number, LA: leaf area (cm2 per plant), TW: total dry weight (g, per plant), AW: aboveground dry weight (g, per plant), SRW: storage root weight (g, per plant) and storage root number.**

| Cultivar | UV-B | VL | VNN | LA | TW | AW | SRW | SRN |
|---|---|---|---|---|---|---|---|---|
| | kJ m-2 d-1 | cm | per plant | cm2 per plant | g, per plant | g, per plant | g, per plant | per plant |
| BG | 0 | 463.67 | 54.00 | 12150.08 | 235.94 | 149.39 | 78.843 | 7.33 |
| | 5 | 393.50 | 48.00 | 4868.76 | 218.66 | 144.24 | 66.681 | 3.33 |
| | 10 | 282.33 | 44.33 | 5841.06 | 88.61 | 60.6 | 76.19 | 3.17 |
| | ANOVA | ns | ns | * | * | * | ns | * |
| HT | 0 | 290.50 | 57.00 | 6008.77 | 122.19 | 83.02 | 36.7 | 6.33 |
| | 5 | 339.33 | 52.83 | 6610.83 | 152.1 | 99.32 | 49.23 | 5.17 |
| | 10 | 338.17 | 60.67 | 6544.7 | 158.37 | 104.02 | 59.93 | 6.33 |
| | ANOVA | ns | ns | * | ns | ns | ns | ns |
| LA | 0 | 320.33 | 57.50 | 5002.55 | 165.99 | 97.42 | 73.72 | 8.67 |
| | 5 | 315.83 | 59.67 | 2884.51 | 134.81 | 97.97 | 34.88 | 3.83 |
| | 10 | 260.50 | 53.00 | 3816.49 | 182.28 | 123.21 | 51.12 | 6.33 |
| | ANOVA | ns | ns | * | ns | ns | ns | * |
| | UV-B | * | ns | *** | ** | * | ns | * |
| | Cultivar | * | ns | *** | ns | ns | ns | ns |
| | UV-B x Cultivar | ns | ns | *** | * | ns | ns | ns |

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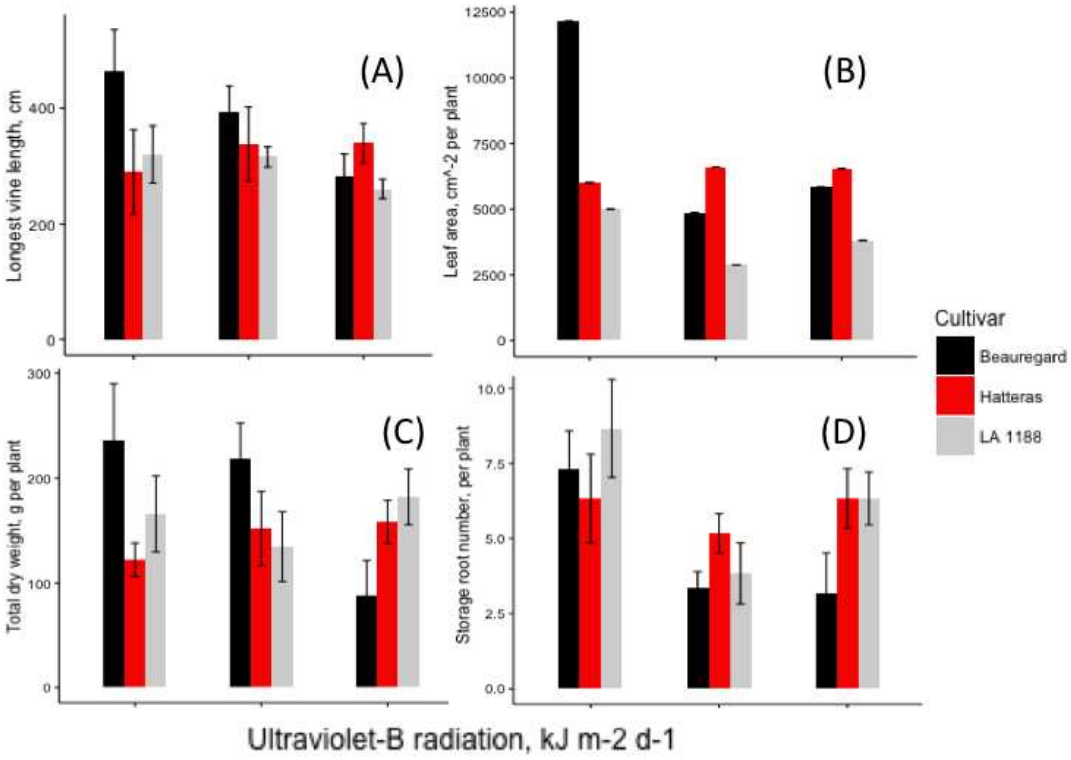


**Figure 5: Effect of Ultraviolet-B radiation (0, 5, 10 kJ $m^{-2}$ $d^{-1}$ UV-B) on (A) longest vine length, cm; (B) leaf area, $cm^2$ per plant; (C) total dry weight, g, per plant; (D) and storage root number of three cultivars (Beauregard, Hatteras, Louisiana 1188). Bars indicate standard errors of the six replications.**

Similarly, leaf area was also significantly affected by UV-B radiation ($P<0.001$) and cultivar difference ($P<0.0001$) (Table 3). UV-B significantly decreases leaf area with maximum decline for BG at projected and LA at ambient UV-B. Leaf area of sweetpotato cultivars grown in control group is 12150 $cm^2$ (BG), 6009 $cm^2$ (HT) and 5003 $cm^2$ (LA). Compared to the control group, ambient and projected UV-B treatment decreases leaf area by 52 and 60% for BG, and 42 and 24% for LA, respectively (Figure 5 B). Again, HT shows an opposite trend that the leaf area under ambient and projected UV-B increase 10 and 9% compared to the control, respectively. Leaf dry weight was significantly affected by UV-B ($P<0.05$) (Table 3). Averaged over cultivars, leaf dry weight in control group is 36 g, which decreases by 26 and 31% under ambient and projected treatment, respectively.

UV-B ($P<0.01$) significantly affected total dry weight (Table 3). Averaged over cultivars, ambient and projected UV-B treatment significantly decreases total dry weight by 4 and 18%, respectively (Figure 5 C). Compared to control group, cultivar BG and HT showed greatest reduction by 62% and 30% under projected UV-B. Cultivar LA showed greatest reduction by 20% under ambient UV-B.

Storage root number was significantly affected by UV-B ($P<0.05$) (Table 3). Averaged over cultivar, storage root number in control group is 7.4, which is significantly reduced with maximum decline under ambient by 45%, and projected treatment by 29% (Figure 5 D).

**Combined response index (CRI) and UV-B sensitivity index (USI)**

The CRI, as an integration of the UV-B effect on sweetpotato vine length, leaf area, node number, total biomass, and storage root dry weight, indicated the sensitivity of sweetpotato cultivars to enhanced UV-B. The result showed that cultivar HT had a positive USI (6.14), and cultivar BG had a greater negative USI (-17.14) than cultivar LA (-4.04),

which classified BG as UV-B-sensitive, and HT and LA as UV-B-tolerant, respectively (Figure 6).

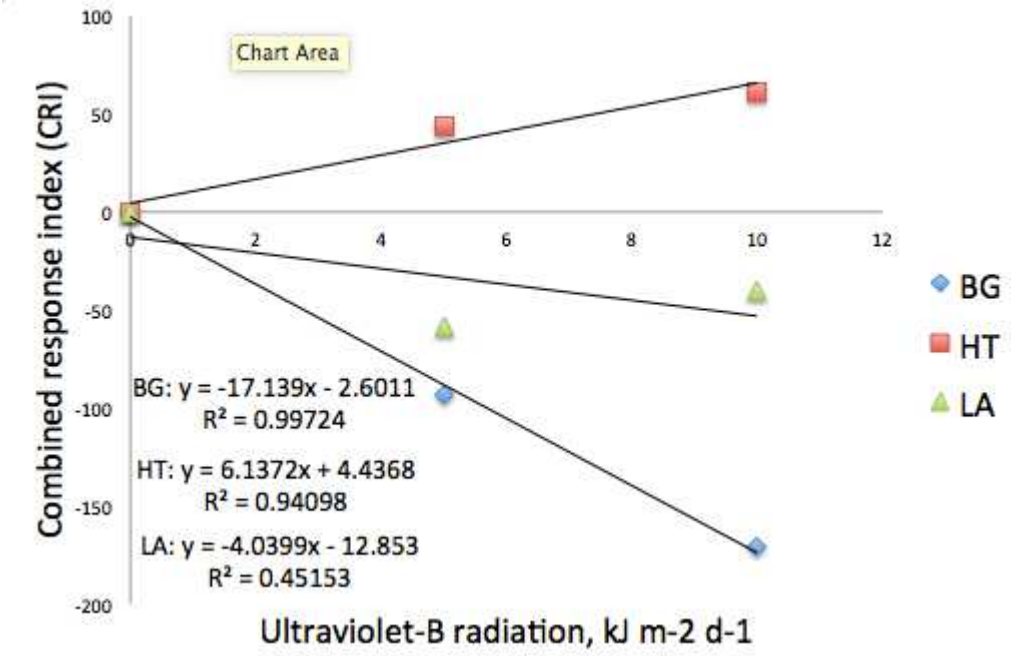


**Figure 6: Combined response index (CRI), which sums the relative responses in vine length, vine node number, leaf area, total dry weight, and storage root dry weight due to UV-B radiation regressed over respective levels of UV-B radiation in three sweetpotato cultivars (BG, HT and LA).**

## DISCUSSION

Our result suggest that the UV-B radiation exposure has significant negative effects on sweetpotato growth (Table 3). For cultivars BG and LA, the vine length, the leaf area and the total biomass went down with the increasing UV-B. Similar reductions in plant heights, leaf areas, and total biomass induced by UV-B have been reported on cotton (Zhao 2003; Gao 2003), maize (Wijewardana 2016; Reddy 2013; Tevini et al. 1991; Mark and Tevini 1997), rice (Coronel et al. 1990; Barnes et al. 1993; Dai et al. 1994a; Dai et al. 1994b), soybean (Koti 2007; Reed et al. 1992), and pea (Gonzalez et al. 1996). The reduction in vine lengths and leaf areas may be caused by the alternation in biosynthesis of some hormones and decrease in cell wall loosening due to the UV-B (Saile-Mark and Tevini 1997). The correlated reduction in total biomass and photosynthesis rates suggest that the biomass loss

may be due to the limitation in productivity. Although the storage root weight was not significantly affected by UV-B, the storage root number was. The ambient UV-B reduced the storage root number the most, and the projected UV-B somehow stimulated the development of the storage root during the early age. However, cultivars HT, which was released in recent years, has some completely different characteristics and responses to UV-B that we have not studied thoroughly. For example, the vine length, leaf area, and total biomass of cultivar HT increased with the increasing UV-B. Similar tend had been found on brood bean and wheat (Al-Oudat et al. 1998). This suggests that the UV-B effect is species/cultivars specific and sometimes it is more than just a distress, but also a eustress (Hideg 2013). The photosynthesis rate of BG was negatively correlated with UV-B, but HT and LA had the maximum values under the ambient and projected UV-B respectively, demonstrating their UV-resistance potentials. Because photosynthetic organs such as chloroplast are UV-B sensitive targets, it was speculated that UV-B reduces photosynthesis by damaging photosynthetic organs and resisting stomatal activity (Nogués 1999). The loss of biomass in our experiment may be also due to the inhibited stomatal activity.

On visual observation, the wax tubes were more abundant and denser under the ambient UV-B and almost disappeared under the projected UV-B (Figure 4). Other studies have found similar results of increased wax tubes on pea and cotton leaves (Kakani 2003; Corlett 1997). The similar result is also support by Figure 4 that showed epicuticular wax morphology on leaf surfaces of sweet-potato exposed to the control (A, B, C), the ambient UV-B (D, E, F) and the projected UV-B (G, H, I). Averaged over cultivars, the wax tube density increased when exposed to the ambient UV-B and decreased when exposed to the projected UV-B. The elevated UV-B stimulated leaf to produce more wax content and the negative effect observed under the projected UV-B may be due to the critical UV-B damage on epidermal cell. Therefore, UV-B sensitivity threshold for sweet-potato leaves should be

between 5 and 10 kJ $m^{-2}$ $d^{-1}$. The epidermal ultrastructures also differ in the cultivars. Under the ambient UV-B, the cultivar HT (B, E, H) showed fewer wax tubes than BG (A, D, G) and LA (C, F, I), indicating that HT might not adapt well to the ambient environment than the other two cultivars. Under the projected UV-B, the cultivar LA showed the complete guard cells while the other two experienced serious damages, indicating that LA have a better chance to survive if UV-B keeps increasing. The experiment result () indicated that the change of wax content was caused by UV-B alone, not by any other stress factors.

Finally, the combined response index (CRI) was an indicator to classify the sweetpotato cultivars BG, HT, and LA into sensitive, moderately sensitive and tolerant to the ambient and projected UV-B. The method had also been used to classify the UV-B sensitivity of rice (Dai 1994) and soybean (Koti 2004), though some modification had been added on their equations.

# CHAPTER III: INTERACTIVE EFFECTS OF ULTRAVIOLET-B RADIATION AND NITROGEN NUTRITION ON SWEETPOTATO GROWTH AND DEVELOPMENT

## INTRODUCTION

The UV-B radiation would continue to stay at a high level in until the mid of next century because of the remaining ozone depletion substance in the atmosphere, in spite of the success of Montreal Protocol (Björn 2008; McKenzie 2011). Elevated UV-B radiation has negative effects on the plants growth and development such as biomass loss, growth reduction, photosynthesis inhibition, and secondary metabolism stimulation (Singh 2013; Koti 2007; Jansen 1998).

Sweetpotato (Ipomoea batatas), as one of the seventh major food crop in the world, contributed more than $500 million to the U.S economy in 2012 (USDA 2013). Previous researches had revealed that soil moisture, soil and air temperature, nitrogen (N) fertilizer, and UV-B radiation significantly influence sweetpotato growth and development (Meyers 2014; Chen 2017). For example, Villagarcia (1998) found that the N-stress (2 nM NO3-) treatment showed a greater net assimilation rate, nitrogen use efficiency (NUE) and dry matter allocation to sweetpotato storage root (root: shoot ratio) than the N-replete (8 mM NO-3) treatment. Chen (2017) investigated the single UV-B effects on sweetpotato and found that the projected UV-B exposure (10 kJ m-2 d-1) reduced the leaf area by 32-54% and the total biomass by 30-62% but increased the leaf wax and phenolics.

Since it is common that plants' response to UV-B depends on other environmental factors such as light, temperature, drought, containments and nutrient limitations (Tevini, 1994; Caldwell 1998), previous studies also conducted experiments to explore the interactive effect of UV-B and other environmental factors on plants (Correia 2000). For example, the interactive effect of UV-B and nitrogen had been studied for maize (Correia 2005) and

common beans (Riquelme 2007). However, no one ever studied such interactive effect on sweetpotato.

To understand the interactive effect of UV-B and nitrogen on sweetpotato growth and development, one experiment was conducted in the greenhouse located at the Rodeney Foil Plant Science Research Center, Mississippi State University. Two UV-B levels (0 and 10 kJ m-2 d-1) were imposed to simulate no UV-B and projected UV-B in Mississippi and three nitrogen levels (100, 60, and 20% of standard Hogland's solution) were imposed to simulate optimal nitrogen, moderate nitrogen-deficiency and severe nitrogen-deficiency conditions. The objective of this study was to examine the interactive effect of nitrogen and UV-B radiation on sweetpotato (B-14) growth and development. We hypothesized that the magnitude and direction of sweetpotato (B-14) response to single UV-B or nitrogen would be modified by the interactive effect between them.

## MATERIALS AND METHODS

**Experiment site:**

This experiment was conducted in a greenhouse covered with UV-B opaque plastic sheeting located at the Rodney Foil Plant Science Research Center, Starkville, Mississippi, USA, from August to November 2016. In the greenhouse, pots with plants were arranged in parallel tables. On the top of each table, UV-B rack with eight lamps was suspended from the metal frames attached to the greenhouse frame work. Ultraviolet-b opaque plastic sheeting was suspended along with the edges from the top of the greenhouse to 10-cm below the table bench so that all plants in teach table were covered by plastic sheeting to filer UV-B coming from the UV-B treatment.

**Plant culture:**

Field-grown sweetpotato slips, slips Nearly two hundred Beauregard (B-14) sweetpotato slips were collected in Chase, LA, on the Sweetpotato Field Day (August 24,

2016). Ninety-six slips were selected among them. Same as described in experiment 1, two nodes with leaves aboveground and two nodes without leaves belowground were kept to make slips uniform. Sandy soil loam mixed with 75% sands and 25% topsoil by volume filled ninety-six PVC pots, then fully saturated with water. Four plants were harvested in each treatment on 10, 20, 40, and 70 DAP to assess plant growth and development.

**Treatment:**

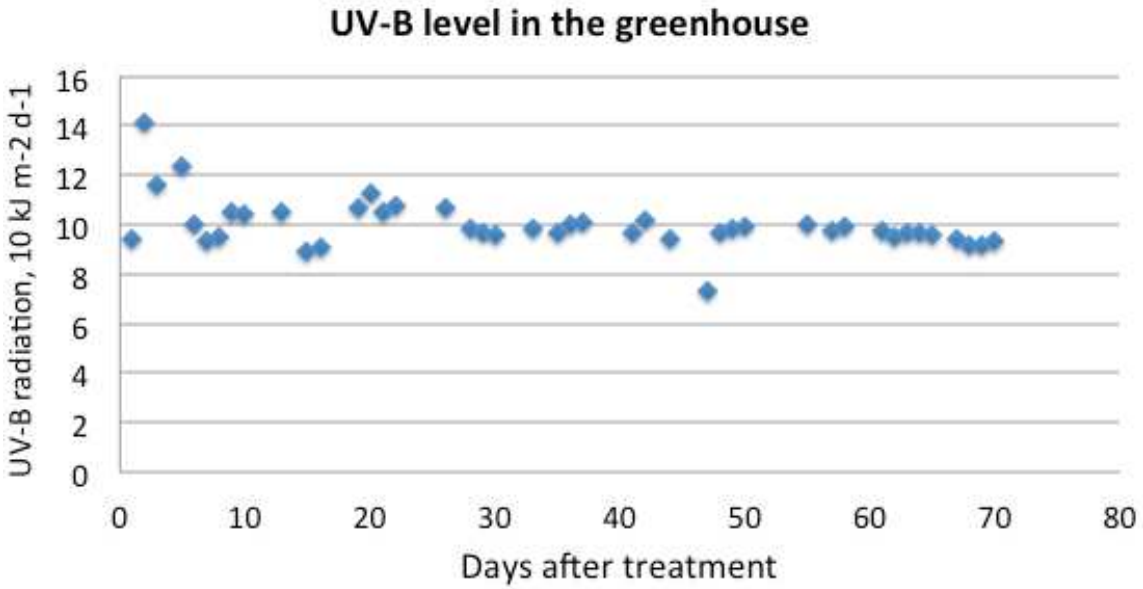


**Figure 7: Daily UV-B radiation level in the greenhouse monitored using a UVX digital radiometer at noon.**

The treatments imposed consisted of two levels of UV-B radiation (0 and 10 kJ $m^{-2}$ $d^{-1}$) and three treatments of nitrogen nutrition (100, 60, and 20% of Standard Hoagland's solution). All the treatments were imposed at planting and continued up to 70 days. UV-B radiation was provided on plants from 0800 to 1600 h each day by a square-wave UV-B supplementation system composed of 10 fluorescent UV-313 lamps (Q-Panel Company, Cleveland, OH, USA) driven by 40 W ballasts in this study under near ambient PAR in the greenhouse conditions. To filter UV-C (< 280 nm) radiation, each lamp was wrapped with pre-solarized 0.08 mm cellulose diacetate film, which is changed every two weeks. The UV-B rack height was adjusted, as needed, to maintain the appropriate UV-B radiation level in

treatment. The mean UV-B dosages averaged over three different locations in the treatment corresponding to the permanent rows for the treatment during the experimental period was 10 kJ. To make sure that the amount of UV-B energy delivered at the canopy of the plant was uniform, a UVX digital radiometer (UVP Inc., San Gabriel, CA, USA) was used to check every day at noon.

For delivering variable nitrogen levels, three individual tanks filled with nutrient solution that substitutes $CaCl_2$ for $Ca(NO_3)^2$ were used to provide the respective different N concentrations nutrient solutions upon imposition of the treatments.

**Phenolic and leaf wax content measurements:**

Three leaves per plant and four plants per treatment were collected on 60 and 70 DAP to determine the concentration of pigments and phenolic compounds. Five leaves discs with a total of 0.38 $cm^2$ leaf area from 3 leaves per plant were punched (punch 3) and placed in the 10 ml phenol reagent (79:20:1 of methanol, distilled water, and HCl) for phenolic content estimation. The leaves used were the fourth or fifth leaf from tip, which was recently expended leaf, were used. Vials were placed in the room temperature and dark for 24 hours to allow the complete extraction of phenolic compounds. The absorbance was solution was measured at 320 nm using the Bio-Rad Smart Spec 3000 spectrophotometer.

Leaf epicuticular waxes content was measured by the similar way. Twenty leaf discs (a total of 35.36 $cm^2$ leaf area) with a size 9 leaf punches were placed in a beaker with 15 ml of chloroform and stirred for 20 s. Then, the chloroform extract was evaporated in a forced air over set at 55 o C, and evaporated completely. To this, 5 mL potassium dichromate reagent was added and placed on a water bath at 80 oC for 30 minutes. After solution was cooled at room temperature, then 12 mL of de-ionized water was added, and the intensity was read at 590 nm as described in Ebercon et al. (1977).

**Growth, developmental and physiological measurements:**

Longest vine length (VL), node number (NN), lead area (LA), leaf dry weight (LW), total biomass (TW), storage root dry weight (SRW) and number (SRN) were measured on 10, 20, 40, and 70 DAP by harvesting four plants in each treatment. Vine length was measured from the base to the recently unfolded leaf on the main branch. Leaf numbers were counted on the main vine. Leaf area was estimated using LI 3100 leaf area meter (LiCor, Inc., Lincoln, NE). Storage root numbers were counted based on the color and enlargement of the adventurous roots in all plants at each harvest. Plant component dry weights were estimated by drying the material in a forced-air over set at 80 $^{o}$C for 72 hours.

Leaf net photosynthetic rates (Pn), stomal conductance, transpiration rate and chlorophyll fluorescence were measured on the forth/fifth uppermost fully expanded mainstem leaf from four plants in each treatment between 1000 and 1200 h using a LI-6400 portable photosynthesis system (Li-Cor Inc.) at 55 and 65 DAP. During the measurements, relative humidity was set to 50%; temperature was set to 30 $^{o}$C based on the temperature in the leaf cuvette; $CO_2$ was set to 410 ppm, greenhouse environment; air flux was set to 400 μmol $s^{-1}$; saturation point was set 1500 μmol m-2 s-1. It often took four minutes to wait the total coefficient of variation (%CV) to reach a value below 0.5% before recording the parameters.

Total relative chlorophyll content was measured usinging a SPAD 502 Plus Chlorophyll Meter on three days, 19, 39, and 69 DAP. For these measurements, recently fully expanded leaves, third or fourth leaf from the top on the main vine, were used. From each leaf, three reading were taken avoiding main veins in the middle of the leaf blade and averaged. Four plants were used for each treatment during the measurement days. .

**Statistical analysis:**

The physiological and growth parameters were analyzed with two-way ANOVA to test the significance of UV-B radiation, nitrogen and their interactions using R-studio and LSD ($\alpha<0.05$) was used to compare the difference between treatment means. A linear regression equation ($y=ax+b$) was used to fit growth data (VL, LA, SRW and TW) with time (DAE) using EXCEL. The longest vine expansion rate (VER), leaf area expansion rate (LAR), total biomass accumulation rate (TBAR) and storage root biomass accumulation rate (SRBAR) were calculated for each harvesting except the first time and the slopes (c) of the linear model ($y=cx+d$) was used as the estimates of VER, LAR, TBAR and SRBAR.

## RESULTS

**Photosynthesis**

UV-B radiation significantly decreased photosynthetic rate ($P<0.05$) and leaf water-use efficiency ($P<0.01$) at 55 DAP (Table 4). Over average nitrogen level, photosynthetic rate was 34.5 μmol $CO_2$ $m^{-2}$ $s^{-1}$ and 26.7 μmol $CO_2$ $m^{-2}$ $s^{-1}$ under control and projected UV-B, respectively, which showed significant reduction by 23% (Figure 8 A). Water-use efficiency in average nitrogen level were 2.76 μmol $CO_2$ $m^{-2}$ $s^{-1}$ and 2.09 μmol $CO_2$ $m^{-2}$ $s^{-1}$ under control and projected UV-B, respectively, which showed significant 24% reduction.

Meanwhile UV-B, nitrogen level and interactive effect of UV-B and nitrogen significantly affect stomatal conductance ($P<0.001$, $P<0.01$, $P<0.01$) and transpiration ($P<0.05$, $P<0.001$, $P<0.01$). Stomatal conductance decreased with increasing nitrogen level under control group, but increases with it under projected UV-B (Figure 8 B). Compared to the control group, stomatal conductance decreases by 24% under projected UV-B. Transpiration rate significantly increases with growing nitrogen under both UV-B treatments with the maximum growth (22%) under control group.

**Table 4: Effect of Ultraviolet-B radiation (0, 10 kJ $m^{-2}$ $d^{-1}$) and nitrogen level (20, 60, 100%) on photosynthesis (Pn), stomatal conductance (Cond), transpiration rate (Tr) and water-use efficiency (WUE) on the forth/fifth fully expended leaf at 55 DAP; and Fv'/Fm', Spad value at 69 DAP; and phenolic and wax at 60 DAP.**

| UV-B | Nitrogen leve | Pn | Cond | Tr | WUE | Fv'/Fm' | Spad value | Phenolic | Wax Content |
|---|---|---|---|---|---|---|---|---|---|
| kJ m-2 d-1 | % | nol CO2 m-2 s | ol H2O m-2 s | nol H2O m-2 s | nol CO2 m-2 s-1 | | µg cm-2 | µg cm-2 | µg mm-2 |
| 0 | 20 | 34.08 | 1.29 | 11.55 | 2.96 | 0.71 | 43.95 | 156.35 | 0.47 |
| | 60 | 34.9 | 1.05 | 12.1 | 2.88 | 0.71 | 46.96 | 156.08 | 0.42 |
| | 100 | 34.5 | 0.88 | 14.05 | 2.45 | 0.71 | 47.09 | 138.51 | 0.67 |
| 10 | 20 | 25.3 | 0.71 | 12.45 | 2.04 | 0.71 | 47.36 | 144.72 | 0.25 |
| | 60 | 25.68 | 0.82 | 13 | 1.98 | 0.71 | 49.81 | 144.89 | 0.33 |
| | 100 | 29.1 | 0.91 | 13 | 2.24 | 0.71 | 49.26 | 156.23 | 0.31 |
| ANOVA | | | | | | | | | |
| | UV-B | * | *** | * | ** | ns | *** | ns | ns |
| | N | ns | ** | *** | ns | ns | *** | ns | ns |
| | UV-B x N | ns | ** | ** | ns | ns | ns | ns | ns |

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 ''

**Table 5: Effect of Ultraviolet-B radiation (0, 10 kJ m-2 d-1 UV-B) and nitrogen level (20, 60, 100%) on VL: vine length (cm), VNN: vine node number, LA: leaf area (cm2 per plant), LW: leaf dry weight (g, per plant), TW: total dry weight (g, per plant), AW: aboveground dry weight (g, per plant), SRW: storage root dry weight (g, per plant), SNN: storage root number and Root/shoot ratio of the sweetpotato at 70DAP.**

| UV-B | Nitrogen | VL | VNN | LA | LW | TW | AW | SRW | SRN | Root/Shoot |
|---|---|---|---|---|---|---|---|---|---|---|
| kJ m-2 d-1 | % | cm | per plant | cm2 per plant | g, per plant | g, per plant | g, per plant | g, per plant | per plant | |
| 0 | 20 | 227.25 | 27.5 | 1253.35 | 5.85 | 57.84 | 17.26 | 37.71 | 8 | 2.4 |
| | 60 | 242.00 | 30 | 2303.38 | 10.14 | 68.47 | 24.61 | 40.5 | 6 | 1.9 |
| | 100 | 215.00 | 29 | 2707.38 | 11.59 | 87.05 | 29.14 | 53.71 | 9.5 | 2.18 |
| 10 | 20 | 152.50 | 24.5 | 1115 | 4.89 | 35.89 | 11.43 | 22.15 | 6 | 2.29 |
| | 60 | 228.75 | 31.5 | 2010.95 | 9.73 | 43.71 | 22.08 | 18.03 | 7 | 1 |
| | 100 | 251.00 | 36.75 | 2078.16 | 10.22 | 49.59 | 24.98 | 20.87 | 4.75 | 1.09 |
| ANOVA | | | | | | | | | | |
| | UV-B | * | ns | ns | ns | ** | ns | * | ns | ns |
| | N | ns | ns | *** | ** | ** | * | ns | * | ns |
| | UV-B x N | ns | ns | ns | ns | ns | ns | ns | ** | ns |

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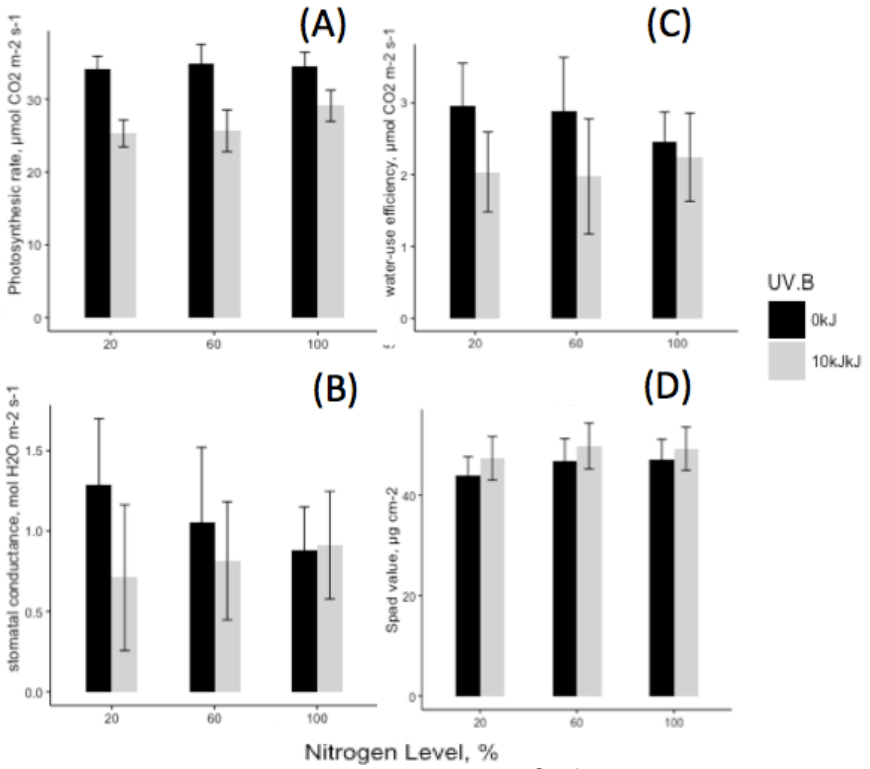


**Figure 8: Effect of Ultraviolet-B radiation (0, 10 kJ $m^{-2}$ $d^{-1}$ UV-B) and nitrogen level (20, 60, 100%) on (A) photosynthesis (Pn), (B) stomatal conductance (Cond), (C) wax content and (D) Spad value (total chlorophyll content) on the forth/fifth fully expended leaf. Bars indicate standard errors of the four replications for Pn, Cond and wax content, and eight replications for Spad value.**

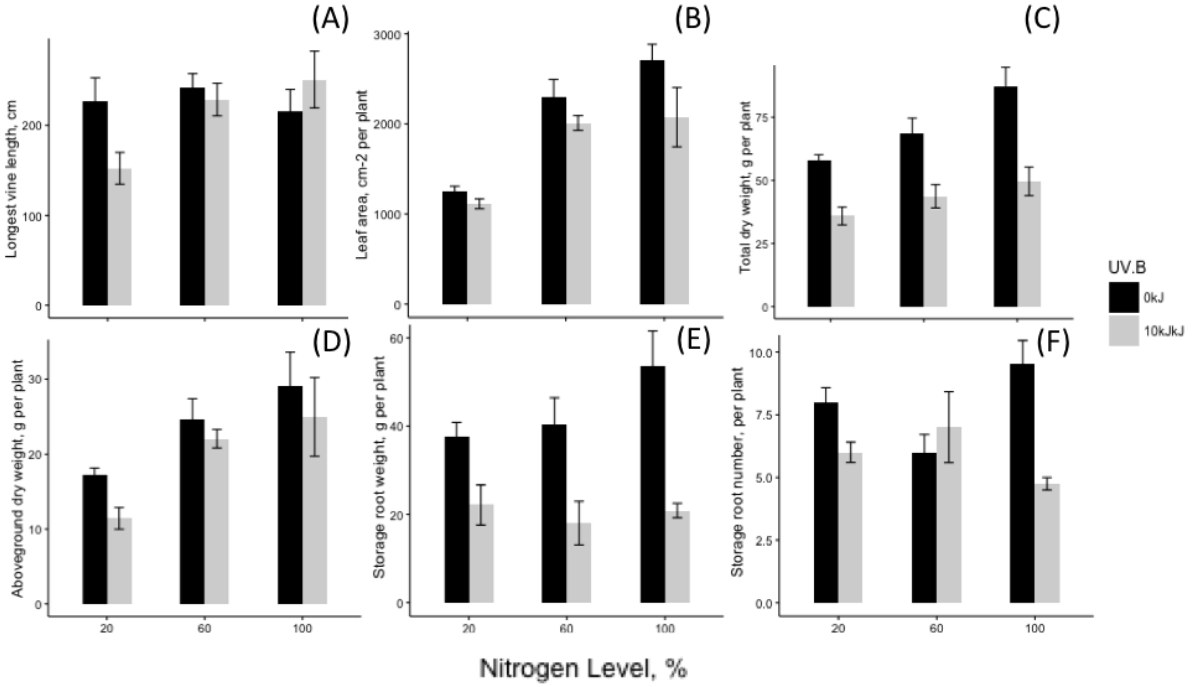


**Figure 9: Effect of Ultraviolet-B radiation (0, 10 kJ $m^{-2}$ $d^{-1}$ UV-B) and nitrogen level (20, 60, 100%) on (A) longest vine length, cm; (B) leaf area, $cm^2$ per plant, (C) total weight, g, per plant, (D) aboveground dry weight (g, per plant), (E) storage root dry weight (g, per plant), and (F) storage root number (per plant). Bars indicate standard errors of four replications.**

**Florescence, Chlorophyll, phenolic and wax**

The chlorophyll content, measured and expressed as SPAD units, which represented total chlorophyll content, was significantly increased by UV-B ($P<0.001$) and nitrogen level ($P<0.001$). The average Spad value were 46 and 49µg $cm^{-2}$ under control and projected UV-B, respectively, thus UV-B significantly increased spad value by 6.5%. Compared to the optimal nitrogen level, nitrogen deficiency (20%) also significantly decreased spad value by 6.7% and 4% under control and projected UV-B, respectively (Figure 8 D).

**Growth and development**

On 70 DAP, longest vine length was significantly affected by UV-B radiation effect ($P<0.05$) (Table 5). Averaged over nitrogen levels, longest vine lengths of sweetpotato were 228 cm (control: 0 kJ $m^{-2}$ $d^{-1}$) and 211 cm (projected: 10 kJ $m^{-2}$ $d^{-1}$) (Figure 9 A), so the projected UV-B decreased vine length by 7%. The combined effect of 20% of N and projected UV-B reduced longest vine length by 29%, compare to the optimal N and 0 UV-B treatment. The vine expansion rate (VER) showed a similar pattern that VER was 8.7% lower under 10 kJ $m^{-2}$ $d^{-1}$ UV-B compared to the 0 UV-B averaged over nitrogen (Figure 10 A).

Nitrogen level significantly decreased the leaf area ($P<0.001$) with maximum decline at the 20% nitrogen level for both control and projected UV-B treatments (Figure 9 B). The leaf areas of sweetpotato grown under the optimal nitrogen (100%) were 2707 $cm^2$ (control) and 2078 $cm^2$ (projected UV-B). Compared to the optimal nitrogen level (100%), 60% and 20 % of nitrogen deficiency decreased the leaf area by 15% and 54% under 0 kJ UV-B, and 3% and 46% under projected UV-B, respectively. The leaf area expansion rate (LAER) was 32% lower under 10 kJ $m^{-2}$ $d^{-1}$ UV-B compared to the 0 UV-B averaged over nitrogen (Figure 10 B).

Leaf dry weight was significantly decreased by nitrogen level ($P<0.01$) with maximum decline at 20% for both control and projected UV-B. Leaf dry weight of

sweetpotato grown in optimal nitrogen (100%) is 11.59 g (0 kJ $m^{-2}$ $d^{-1}$) and 10.22 g (10 kJ $m^{-2}$ $d^{-1}$). Compared to the optimal nitrogen level (100%), 60 and 20 % nitrogen deficiency decreases leaf dry weight by 13 and 50% for 0 kJ $m^{-2}$ $d^{-1}$ UV-B, and 5 and 52% for control and projected UV-B, respectively.

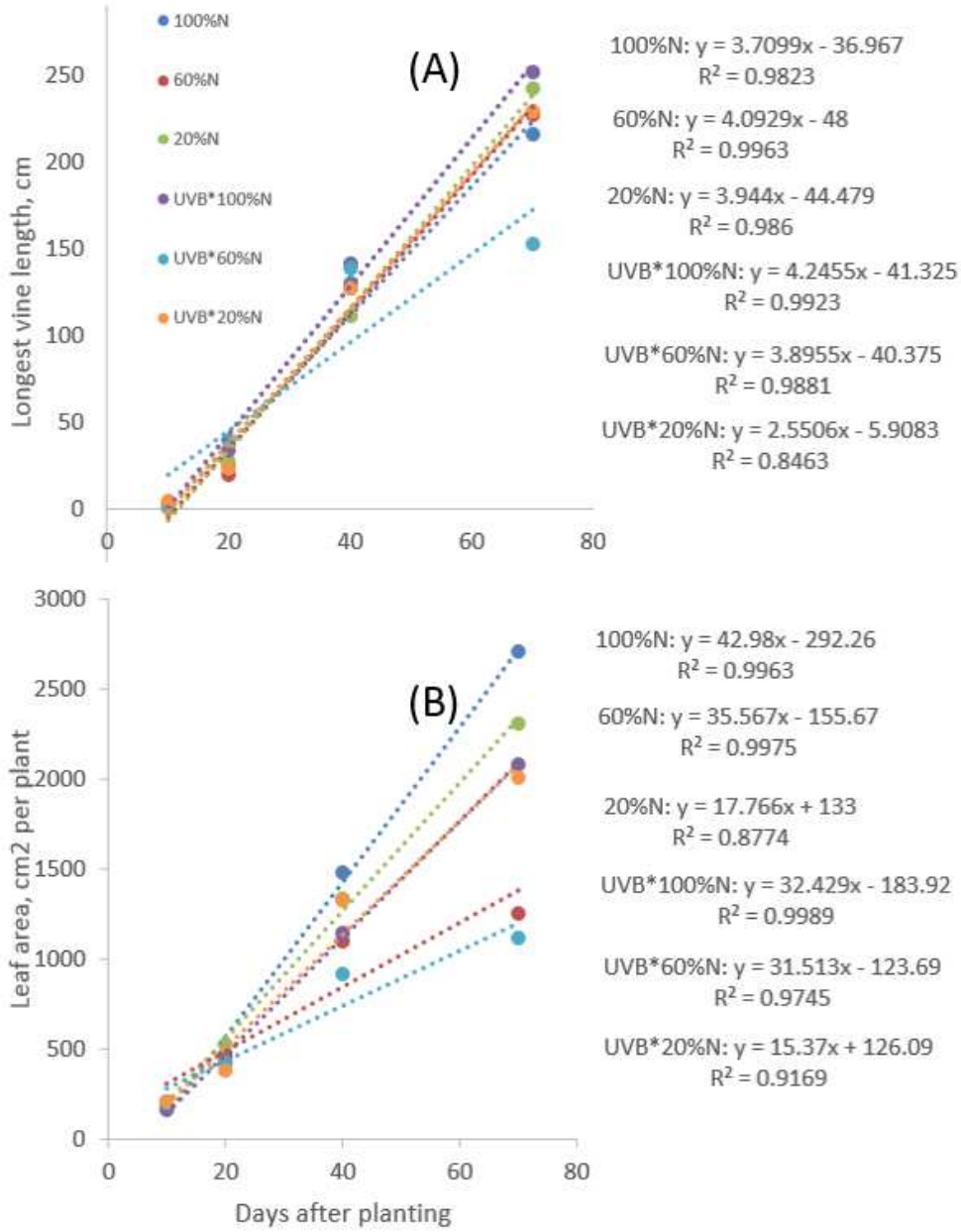


**Figure 10: Time series analysis of sweetpotato cultivar BG (A) longest vine length and (B) averaged leaf area per plant across six treatments.**

Nitrogen level significantly decrease ($P<0.05$) aboveground dry weight with maximum decline at 20% N for control and projected UV-B treatments (Figure 9 D). Aboveground dry weight of sweetpotato grown in optimal nitrogen (100%) is 29.14 g (0 kJ

$m^{-2}$ $d^{-1}$) and 24.98 g (10 kJ $m^{-2}$ $d^{-1}$). Compared to the optimal nitrogen level (100%), 60 and 20 % nitrogen deficiency decreases leaf dry weight by 16 and 41% for 0 kJ $m^{-2}$ $d^{-1}$ UV-B, and 12 and 54% for 10 kJ $m^{-2}$ $d^{-1}$ UV-B, respectively.

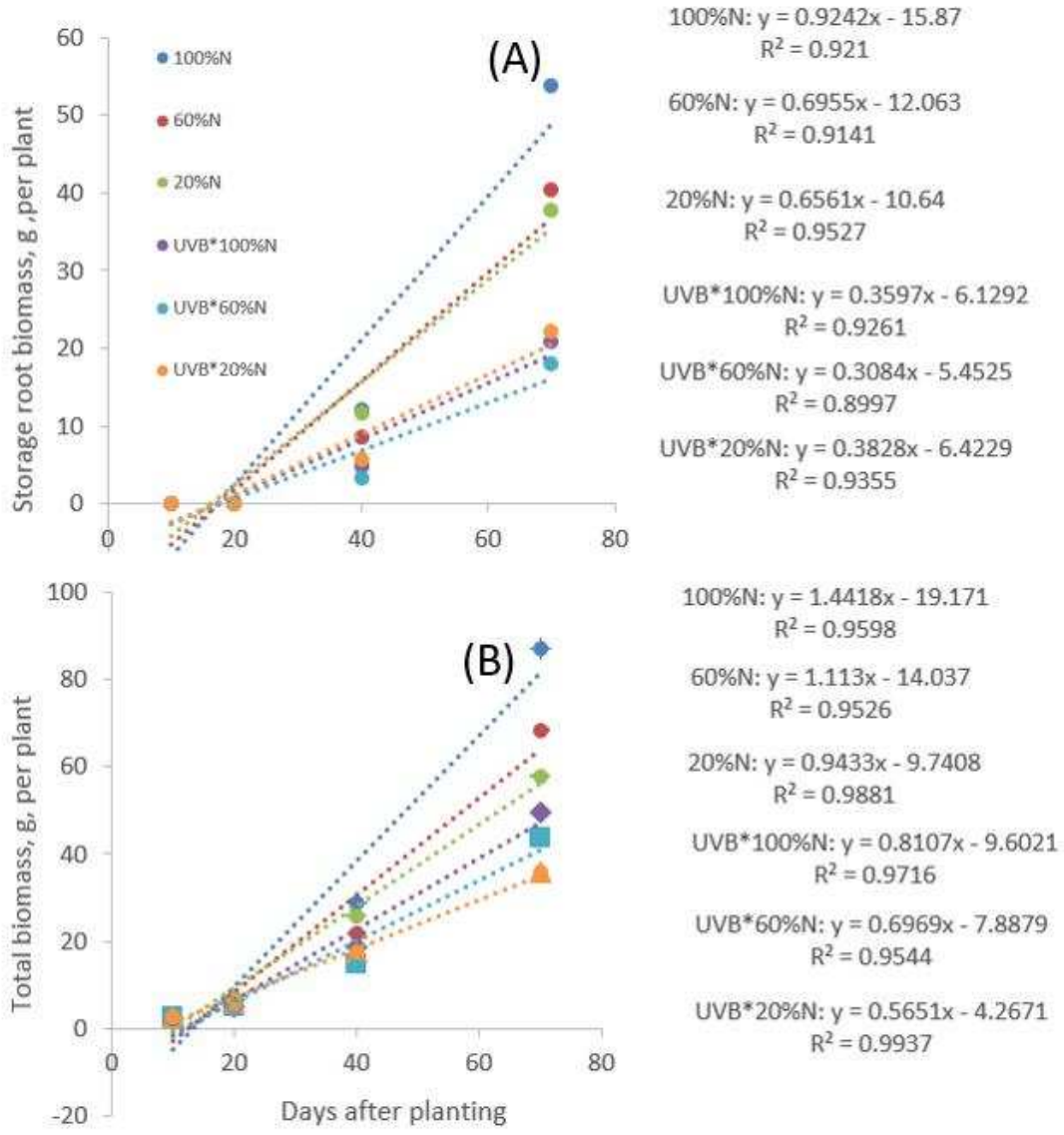


**Figure 11: Time series analysis of sweetpotato cultivar BG (A) averaged storage root weight per plant and (B) averaged total biomass across six treatments.**

Storage root dry weight was significantly affected by UV-B radiation ($P<0.05$). Storage root weight of sweetpotato grown averaged over nitrogen levels is 44 g (0 kJ $m^{-2}$ $d^{-1}$) and 20 g (10 kJ $m^{-2}$ $d^{-1}$) (Figure 9 E). Compared to the 0 kJ $m^{-2}$ $d^{-1}$ UV-B treatment, projected UV-B treatment decreases storage root dry weight by 55%. The combined effect of 20% N-

deficiency and 10 kJ $m^{-2}$ $d^{-1}$ UV-B reduced storage root weight by 59% compare to the optimal N and 0 UV-B treatment. The storage root biomass accumulation rate (SRBAR) was 54% lower under 10 kJ $m^{-2}$ $d^{-1}$ UV-B compared to the 0 UV-B averaged over nitrogen (Figure 11 A). The combined effect of UV-B and 20% of N-deficiency enhanced the reduction of SRBAR to 59% compared to the 0 UV-B and optimal nitrogen treatment.

Effect of UV-B ($P<0.01$) and nitrogen level ($P<0.01$) significantly differed in total dry weight (total biomass). Total dry weight significantly decreases averaged over nitrogen level with maximum decline at 39% between 0 and 10 kJ $m^{-2}$ $d^{-1}$ UV-B (Figure 9 C). Total dry weight of sweetpotato grown in optimal nitrogen (100%) is 87.05 g (0 kJ $m^{-2}$ $d^{-1}$) and 49.59 g (10 kJ $m^{-2}$ $d^{-1}$). Compared to the optimal nitrogen level (100%), 60 and 20 % nitrogen deficiency decreases leaf dry weight by 21 and 34% for 0 kJ $m^{-2}$ $d^{-1}$ UV-B, and 12 and 28% for 10 kJ $m^{-2}$ $d^{-1}$ UV-B, respectively. Meanwhile, 20% N-deficiency and 10 kJ $m^{-2}$ $d^{-1}$ UV-B reduced total weight by 59% compare to the optimal N and 0 UV-B treatment. The total biomass accumulation rate (TBAR) was 40% lower under 10 kJ $m^{-2}$ $d^{-1}$ UV-B compared to the 0 UV-B averaged over nitrogen (Figure 11 B). The combined effect of UV-B and 20% of N-deficiency enhanced the reduction of BAR to 60% compared to the 0 UV-B and optimal nitrogen treatment.

Interactive effect of UV-B and nitrogen was only observed on storage root number. Swetpotato grown in optimal nitrogen level and 0 kJ $m^{-2}$ $d^{-1}$ UV-B had significantly more (26%) storage roots ($P<0.01$) than those in 20% nitrogen and projected UV-B treatment (Figure 9 F).

## DISCUSSION

The single UV-B factor were observed to significantly influence the growth and development of sweetpotato. Regardless of nitrogen levels, UV-B decreased most growth parameters with the greatest effect at 20% of nitrogen deficiency, compared to the 100 and

60% nitrogen. The reduction in vine lengths, leaf areas, storage root biomass, and total biomass may be due to the reduction in their growth rate (VLER, LAER, SRBAR and BAR). Reduction of plant heights and photosynthesis rates induced by UV-B radiation alone has been reported on cotton (Song 1999; Zhao 2003; Gao 2003), maize (Wijewardana 2016; Reddy 2013; Tevini et al. 1991; Basiouny 1986; and Santos et al. 1993), and rice (Basiouny 1986; Tevini et al. 1991; and Teramura et al. 1984), which may be caused by the alternation in biosynthesis of some hormones stimulated by UV-B; or decrease in cell wall loosening due to UV-B (Saile-Mark and Tevini 1997). UV-B reduction effect in total biomass has been found on soybean (Koti, 2007; and Reed et al. 1992), rice (Barnes et al. 1993; and Dai et al 1994a and Dai et al. 1994b), and wheat (Li et al. 1998). The reduction might be correlated with the UV-B inhibition on leaf photosynthesis (Nogués 2003). However, UV-B did not influence the phenolics and wax content of sweetpotato. Fluorescence parameters such as Fv'/Fm' showed no obvious response to UV-B, expect for the spad value which showed that the total chlorophyll content increased with UV-B (by 6.7%). The increased chlorophyll content may offset the UV-B stress on photosynthesis. Stomata activity was a more sensitive target than electron transportation and Calvin cycle to influence the photosynthesis (Nogués 2006). The potential mechanism is the inhibition of ATP synthesis in guard cells thylakoids, or inhibition of the plasmalemma ATPase proton pump (Nogués 1999), which has been reported in pea and it is suspected that the same pattern also applies to sweetpotato, considering the stomatal conductance was significantly affected by UV-B as well as transpiration and water-use efficiency (Table 4).

The single nitrogen factor showed significant positive effects on sweetpotato's leaf areas, leaf weights and aboveground ground biomass. Nitrogen attributes to the photosynthesis through controlling light absorption and leaf expansion though cell elongation (Radin and Boyer 1982; Correia 2000). More specifically, the nitrogen-deficiency reduces the

stomatal conductance of sweetpotato, which resulted in a reduction in photosynthesis rate. The gap of the stomatal activity and the transpiration rate has been minimized at the optimal nitrogen level, which is critical for production and regeneration of ATP for stomata, or ribulose-1,5-bisphosphate (RuBisCO) for Calvin cycle (Nogués 2006).

It is hypothesized that the magnitude and direction of sweetpotato response to single UV-B or nitrogen would be modified by the interactive effect between them. However, no interactive effect of UV-B and nitrogen had been found on sweetpotato (Table 5) except for storage root number. Similar results had been reported on maize and common beans before that nitrogen fertilization did not change the magnitude and direction of UV-B effect on plants growth (Correia 2000; Riquelme 2007). But the interactive effect of UV-B and nitrogen on RuBisCO and PEPCase activities had been found on maize (Correia 2005). It seems that nitrogen fertilizer management would not be able to avoid UV-B effect on sweetpotato growth.

# CHAPTER IV: GENERAL SUMMARY AND CONCLUSIONS

The objective of this study was to understand the effects of ultraviolet-B radiation on the growth, development and physiology of sweetpotato. Two experiments were conducted to fulfill these objectives. In Experiment 1, three contrasting sweetpotato cultivars, Beauregard, Hatteras, and LA 1188, responses to three levels of UV-B (0, 5 and 10 kJ $m^{-2}$ $d^{-1}$) were evaluated in sunlit plant growth chambers. Plants were grown under these UV-B treatments for 80 days. Growth and developmental parameters were measured at the end of the experiment. Physiological parameters were estimated several days during the course of the experiment. The ambient (5 kJ $m^{-2}$ $d^{-1}$) and projected UV-B (10 kJ $m^{-2}$ $d^{-1}$) of UV-B radiation affected most of the measured growth and physiological parameters. Yield was reduced under ambient and elevated UV-B levels compared to plants with UV-B, possibly due to dysfunction of photosynthesis and reduced whole plant leaf area. Based on combined response index (CRI) and UV-B sensitivity index (USI), Beauregard, the most commonly-grown cultivar in Mississippi was sensitive to elevated UV-B radiation and LA 1188 and Hatteras were classified moderately sensitive and tolerant to current and projected UV-B radiation.

Although both elevated UV-B and nitrogen-deficiency inhibited the growth of sweetpotato, there was no interaction between the two important stressors on growth and physiology of sweetpotato except storage root numbers. The combined effect of UV-B and nitrogen-deficiency reduced vine length and leaf area, and photosynthesis and thus resulting in lower storage root and total biomass. Storage root growth was more sensitive to UV-B compared vine and leaf area growth. The reduction in storage root growth under elevated UV-B and low nitrogen was compared to reductions observed at optimum N levels. This implies that marinating optimum N levels may offset some of the deleterious effects of UV-B. In summary, the current and projected UV-B will have implications for sweetpotato

growth and yield. Significant variability among the cultivars indicates developing UV-B tolerant cultivars will be more productive under current and future UV-B environments. Large-scale genomes to phenomes studies are needed to identify the lines and the genes that are associated with UV-B tolerance and incorporating those traits into region-specific more productive cultivars will benefit the sweetpotato industry.

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