INFLUENCE OF LIGHT QUANTITY AND DURATION, AND TEMPERATURE ON GROWTH AND DEVELOPMENT OF SUCCULENTS

By

Anthony J. Soster

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ABSTRACT

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Succulents have continued to grow in popularity in recent years due to their diverse colors, forms, and suitability as houseplants. However, few if any scientific publications exist on how to optimize growth and promote flowering of the most popular genera. Therefore, the objectives of Expt. 1 were to 1) establish the critical photoperiod for flowering and 2) quantify the interaction of photoperiod and radiation intensity on growth and development of *Echeveria*. In Expt. 2, I wanted to 1) establish if a single paclobutrazol drench could prevent excessive stem elongation in a low light environment and 2) determine the duration of paclobutrazol drenches efficacy. Lastly, in Expt. 3 I quantified the interaction of radiation intensity and day and night temperature on growth and development of seven succulent genera and cultivars. In Expt. 1, DLI and photoperiod interacted to affect the growth index of *Echeveria* 'Apus', 'Canadian', 'Elegans Blue', and 'Jade Point', suggesting that day lengths ≥13-h and DLIs of 5 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ resulted in larger plants, but not higher quality plants compared to those grown under short photoperiods and DLIs of 12 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$. In Expt. 2 plants under low DLIs exhibited an increase in extension growth. However, plants treated with increasing rates of paclobutrazol resulted in reduced stem elongation, even under low DLIs. Lastly, in Expt. 3 growth index increased under moderate DLIs and cooler temperatures for some genera and moderate DLIs and high temperatures for others. These results greenhouse growers with information regarding how succulents respond to the environmental stimuli of photoperiod, temperature, and radiation intensity.

This thesis is dedicated to Donald R. Katz.
Without whom none of this would have been possible.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

SECTION I

Literature Review: Environmental Parameters to Optimize Production of Succulents.

Introduction

The wholesale value of the commercial floriculture industry in the United States (U.S.) was $4.4 billion in 2019, up $50 million from 2015 (USDA, 2019). However, the average growth rate has been relatively stagnant at 2% on a year-by-year basis over the past decade and was down 6% from 2018 to 2019 (USDA, 2019). From 2018 to 2019 the total area of greenhouse crop production increased by 8%, but the number of operations decreased by 19% (USDA, 2019). Not surprisingly, consolidation, increasing competition, and stagnant growth are indicators of a maturing or declining market (Hall, 2006).

Therefore, as competition continues to increase, growers must find ways to differentiate themselves from their competitors by providing increased value to consumers, reducing production costs, taking market share from other producers or by developing completely new markets with innovative and profitable products (Hall, 2006). Methods to increase profitability include reducing energy, production, or labor costs; growing new or popular crops; adopting new technologies; or optimizing the use of existing technologies. Of those, the most promising avenue is to grow alternative, new, or popular crops to develop new markets. This requires growers develop estimates of revenue and expenses by selecting a combination of crops to maximize profits (Wei et al., 2020). For growers to be successful with any crop, research-based production information including how juvenility, radiation duration, intensity, and quality, and temperature influence growth and development must be available (Erwin, 2009).

From 1997 to 2019, the wholesale value of the cacti and succulent market increased from $22 to $70 million (218%) (USDA, 1998; 2019). Sales continue to increase due to their unique appearance, diversity, adaptability, drought tolerance, and ease of maintenance, alongside new varieties, colors, and forms introduced into the market (Armitage, 2016; Machovina, 2017; Wright, 2015). While there are almost 700 genera and over 12,500 species of succulents known (Nyffeler and Eggli, 2010), only about 17 genera of succulents are available for large scale commercial greenhouse and nursery production (Altman Plants, 2021; Ball Seed, 2021; Dümmen Orange, 2020). According to a recent survey of Midwestern U.S. growers, the top 12 succulent genera produced (volume) and sold (sales) include: 1) common aloe (*Aloe*), 2) tree houseleek (*Aeonium*), 3) jade plant (*Crassula*), 4) Mexican hens and chicks (*Echeveria*), 5) ox-tongue (*Gasteria*), 6) graptoveria (*Graptoveria*), 7) zebra cactus (*Haworthia*), 8) kalanchoe (*Kalanchoe*), 9) houseleek (*Sempervivum*), 10) stone crop (*Sedum*), 11) elephant bush (*Portulacaria*), and 12) senecio (*Senecio*) (W.G. Owen, personal communication).

Unlike most other ornamental plants, succulents are slow growing and require unique growing conditions as they are xerophytes that are adapted to arid environments with limited water availability (Das and Panda, 1995). Most are native to Africa, Mexico, Central America, and equatorial latitudes and thrive in mid latitudes (Erwin, 2009; Erwin et al., 2017; Smith, 2019). For this reason, it is difficult to propagate and produce them outdoors in temperate climates, making them highly suitable for greenhouse production. However, limited cultural and environmental research has been conducted and numerous knowledge gaps exist (Erwin et al., 2017).

Classification of succulents can be difficult as there is continued disagreement on the definition of succulence and the term remains colloquial. Succulence can be quantified as a function of water content per unit surface area (Mantovani, 1999). Plants exhibiting this trait generally have a low surface area to volume ratio; however, some tissues have varying degrees of succulence (Griffiths and Males, 2017; von Willert et al., 1990). Succulence may be a continuous trait, existing at varying degrees within tissues and across genera growing in harsh environments (Guralnick and Gladsky, 2017). For example, halophytes are plants that exhibit salt-tolerant adaptations, whereas epiphytes are plants adapted to living on the surface of other plants, and xerophytes are adapted to living in arid regions. Removing halophytes and epiphytes from the classification may be beneficial, as this allows for focusing on xerophytes (Eggli, 2012). Many plants classified as succulents come from the family Crassulaceae; *Aeonium*, round-leafed navel-wort (*Cotyledon*), *Crassula*, *Echeveria*, *Kalanchoe*, pachyveria (*Pachyveria*), *Sedum*, and *Sempervivum*. Gaining a better understanding of how this family responds to manipulation of environmental parameters could have a significant impact on commercial production efficiency and capacity.

Crassulacean Acid Metabolism (CAM) Photosynthesis

Crassulacean acid metabolism (CAM) is a form of photosynthesis used extensively by plants native to arid environments, as it minimizes water loss through transpiration during the night. CAM plants make up about 10% of all higher plants and can be found in diverse biomes ranging from deserts to tropical rainforests (Yamori et al., 2014). CAM is generally characterized by stomatal closure and malic acid accumulation during the day and stomata opening and carbon dioxide (CO_2) accumulation during the night (Kluge and Ting, 1978). It is during the night that CO_2 enters though the stomata and becomes bound to phosphoenolpyruvate carboxylase to form malate, which is then converted into malic acid to be stored until the day to undergo the Krebs cycle, converting malic acid into carbohydrates (Kluge and Ting, 1978). Other organic acids also accumulate during the night, such as oxalacetate, pyruvate and citrate (Kluge and Ting, 1978). The relative concentrations of acid in plant tissues fluctuate throughout the day/night cycle as malic acid is converted into carbohydrates (Buchanan-Bollig, 1984; Kenyon et al., 1981; Moradshahi et al., 1977). By quantifying these fluctuations in acid metabolism, we are able to visualize the effects of environmental conditions on CAM photosynthesis.

Many succulents utilize Crassulacean acid metabolism (CAM) photosynthesis; this is the case for nearly all species in the Crassulaceae family (Ting, 1985). However, CAM photosynthesis is not utilized by all succulents (Ranson and Thomas, 1960). Recent research suggests that CAM photosynthesis, in some species, is a facultative trait; present under drought conditions and absent under wet conditions (Holtum et al., 2017; von Willert et al., 1985; Winter and Holtum, 2017). The conclusion being that some plants exhibit the trait under water-stressed conditions as a survival mechanism. However, plants in submerged aquatic environments can also exhibit CAM photosynthesis, suggesting that CO_2-deficient environments also favor the evolution of CAM (Keeley, 1998).

Temperature has been shown to have an impact on the productivity of CAM plants; specifically, high night temperatures appear to inhibit CAM (Kluge and Ting, 1978). Temperatures above 35 °C eliminate nighttime CO_2 fixation, and shifts metabolism to respiration (Kluge and Ting, 1978). Interestingly, very low night temperatures may also inhibit carbon fixation during the night period. Mother of thousands (*Kalanchoe daigremontiana*) and mother of millions (*K. tubiflora*) showed near zero CO_2 uptake when night temperatures were 5 °C (Kluge, 1969). Optimum night temperatures for most CAM plants appear to range from 15 to 22 °C (Kluge and Ting, 1978). In contrast, warm day temperatures appear to hasten malic acid consumption and decrease gas exchange (Moradshahi et al., 1976). For pineapple (*Ananas comosus*), as temperature increased from 20 to 35 °C, titratable acidity decreased from 20 to 5 meq of acid/100g of fresh weight, suggesting higher temperatures resulted in more respiration

(Moradshahi et al, 1976). These temperature optimums mimic natural temperature fluctuations in an arid environment. Low environmental humidity leads to large temperature swings resulting in low night temperatures and high day temperatures (Balling et al., 1998).

Plant tissue age can also have an impact on the presence of CAM photosynthesis. Jones (1974) found that older leaves of lavender scallops (*Kalanchoe fedtschenkoi*) had more titratable acidity compared to younger tissues on the same plant. Younger leaves appeared to have less overall acidity and varied less in concentration throughout the day/night cycle (Jones, 1974). This work was substantiated by Guralnick et al. (1984), who reported acids associated with CAM were not present in young leaf tissue of elephant bush (*Portulacaria afra*). The study also provided evidence that CAM photosynthesis is favored under long day lengths, as plants grown in growth chambers under a 15-h photoperiod exhibited greater fluctuations in acid concentrations compared to plants grown under a 9-h short day (Guralnick et al., 1984). However, water stress was the most important factor driving the onset of CAM, resulting in the largest fluctuations in acid concentrations (Guralnick et al., 1984).

Photoperiod can have profound effects on development; however, for plants utilizing CAM, there may also be growth effects. For example, growth of century plant (*Agave deserti*), compass barrel cactus (*Ferocactus acanthodes*), and barbary fig (*Opuntia ficus-indica*) increased with increasing photoperiod (Nobel, 1989). A study investigating the effects of leaf age and photoperiod on florist kalanchoe and teddy bear kalanchoe (*K. blossfeldiana* and *K. velutina*) found young leaves of plants grown in growth chambers under a 16-h photoperiod exhibited respiration similar to C_3 plants but exhibited greater rates of CAM as they aged (Brulfert et al., 1982). Additionally, under short day lengths, young leaves exhibited greater CAM photosynthesis than mature leaves under long day lengths (Brulfert et al., 1982). The implications of photosynthetic pathway regulation under different environmental conditions stretch beyond the field of ecology. Many researchers are interested in breeding CAM traits into C_3 crops in lieu of global climate change, as the propensity of CAM photosynthesis for water use efficiency could prove advantageous in the face of prolonged drought and extreme temperatures (Males and Griffiths, 2017). For the greenhouse industry, manipulating the dominate photosynthetic pathway in succulents with environmental cues could lead to increased growth rates and shorter production times.

It is important to note that many of these studies were conducted in growth chambers where photoperiods were created using radiation intensities similar to those used for supplemental lighting. Future studies could investigate whether low-intensity photoperiodic lighting used in the commercial floriculture industry can trigger the same changes in CAM as high-intensity supplemental lighting, and if thresholds of perception for development are the same as the thresholds of perception for growth. Additional research needs to be conducted both in the classification of succulents by their photosynthetic mechanisms, and in understanding how CAM plants adapt to changes in the environment.

Photoperiod

Phytochromes are important photoreceptors and are partly responsible for determining several aspects of plant growth and development including flowering, extension growth, and leaf expansion (Hendricks et al., 1962; Sager et al., 1988). They have photo-reversible isometry; the red (R) radiation absorbing active form P_{660} (P_R), which absorbs radiation from 600 to 700 nm (peak absorption at 660 nm), and the far-red (FR) radiation absorbing inactive form P_{730} (P_{Fr}), which absorbs radiation from 700 to 800 nm (peak absorption at 730 nm) (Hendricks et al., 1962;

Sager et al., 1988). In the presence of FR radiation, or in the absence of R radiation, P_{Fr} will convert to P_R, and in the presence of R radiation, P_R will convert to P_{Fr} (Sager et al., 1988; Thomas and Vince-Prue, 1997).

Under low radiation intensities or R to FR ratio (R:FR), stem elongation can increase dramatically (Smith, 1982). This response can be partially attributed to the affinity for absorption of different wavelengths for photosynthesis; a much greater percentage of FR radiation is either reflected or transmitted through a plant canopy than blue (400 to 500 nm) or R radiation, which have greater photosynthetic efficacy (Franklin and Whitelamb, 2005). Phytochrome photoreceptors of plants below the canopy perceive a low R:FR (Ballare et al., 1990; Ciolfi et al., 2013). When high proportions of FR radiation are detected, phytochromes are translocated to the nucleus in their biologically active form and a cascade of gene responses are initiated, leading to internode elongation (Ciolfi et al., 2013). This is termed the shade avoidance response, whereby plants redirect energy toward internode elongation in an attempt to move new tissues into areas of higher radiation (Smith, 1982).

Photoperiod is the number of consecutive hours of radiation in a 24-hour period. Variations in photoperiod occur naturally due to the tilt of the earth's axis, which creates an approximate 12-/12-h day/night at the equator year-round. At extreme latitudes, 24-h of day or night can occur during parts of the year (Jackson, 2009). Plants are classified by their flowering responses to photoperiod; long-day plants (LDPs) and short-day plants (SDPs) respond to night lengths shorter or greater than a specified critical photoperiod, respectively, whereas day-neutral plants (DNPs) flower regardless of photoperiod (Thomas and Vince-Prue, 1997). LDPs and SDPs can be further categorized as having an obligate or facultative response; requiring a specific photoperiod to induce flowering, or hastening flowering under optimum photoperiods

(Thomas and Vince-Prue, 1997). While photoperiodic classifications refer to the photoperiod as being the mechanism that controls flowering, the flowering of both LDPs and SDPs is dependent upon the duration of the night rather than the day (Thomas and Vince-Prue, 1997). It is the relative accumulation of P_{Fr} and P_R in relation to the length of the night that influences factors such as flowering, stem elongation, and leaf expansion (Franklin and Whitelamb, 2005; Hendricks et al., 1962; Thomas, 1991).

In the commercial floriculture industry, manipulation of photoperiod has become useful in inducing flowering crops out of season. For LDPs, day-extension (DE) lighting can be used to extend the perceived photoperiod during seasons with naturally short photoperiods (Adams and Langton, 2005). Additionally, breaking up the night period with night-interruption (NI) lighting, usually ranging from 1 to 4 hours, can also induce LDPs into flower (Adams and Langton, 2004). Furthermore, SDPs can be induced during long natural day lengths by blocking out radiation with opaque black cloth and truncating the photoperiod (Adams and Langton, 2004).

An observational study on flowering of over 150 South African succulents in conservatories and botanical gardens found that species tended to flower during the same time interval each year, and often near the shortest days of the year (Calle et al., 2010). The authors also found many of the succulents tended to remain dormant during the hot, dry summer (Calle et al., 2010). For some commercially important succulents, short days seem to elicit a greater flowering response in controlled environments. For example, afuoto kalanchoe (*K. glaucescens*), Christmas tree plant (*K. laciniata*), chandelier plant (*K. manginii*), shovel plant (*K. nyikae*), common kalanchoe (*K. rotundifolia*), coral bells (*K. uniflora*), and *K. velutina* are classified as obligate SDPs and will flower in as few as 8 weeks when exposed to 8-h short days (Currey and Erwin, 2011b).

However, radiation intensity may also interact with photoperiod. Garcia (2019) observed several cultivars of basil flowered more rapidly under long days when exposed to high radiation intensities, but under low radiation intensities there was no significant difference in time to flower across photoperiods. Our preliminary research established hens and chicks (*Echeveria* spp.) 'Domingo' exhibited a similar response (Soster and Lopez, unpublished). Nobel (1989) reported that, when the photoperiod increased from 6 to 18 h, the leaf unfolding rate of *Agave deserti* increased by 33%, leaf volume of barbary fig increased by 50%, and height of *Ferocactus acanthodes* increased by 81%. Additionally, *Opuntia ficus-indica* displayed CO_2 uptake of 73, 96, and 112 $mmol\cdot m^{-2}$ under 6, 12, and 18-h photoperiods, respectively (Nobel 1989). These changes in growth, paired with an increase in carbon assimilation, indicate a shift from CAM to C_3 photosynthesis under longer photoperiods (Nobel 1989).

Daily Light Integral

Photosynthetically active radiation (PAR) is the radiation within the wavelengths of 400 to 700 nm that plants utilize for photosynthesis and does not consider FR (700-800 nm) or ultraviolet (UV; ≤400 nm) radiation (Zhen and Bugbee, 2020). Much research has been devoted to the influence of FR radiation on regulating flowering responses through the manipulation of phytochrome and photoperiod (Rockwell et al., 2006), with recent research indicating it also contributes to photosynthesis (Zhen and Bugbee, 2020). UV radiation has been shown to promote secondary metabolites such as phenolics, antioxidants, and anthocyanins (Loconsole and Santamaria, 2021). However, excessively high UV radiation can lead to plant damage, stunting, and reduced quality (Loconsole and Santamaria, 2021). The photosynthetic daily light integral (DLI) refers to the total accumulation of PAR over an entire day (Faust et al., 2005). It can be increased by increasing either the intensity of the radiation delivered or the photoperiod.

For most plants, an increase in DLI results in an increase in root, shoot, and flower biomass accumulation and plant quality (Faust et al., 2005). For example, total dry mass of african marigold (*Tagetes erecta*) 'American Antigua Orange' increased from 2 to over 14 g as DLI was increased from 4.8 to 42.9 mol·m^{-2}·d^{-1} (Faust et al., 2005). Similarly, increasing the DLI from 2.2 to 9.7 mol·m^{-2}·d^{-1} resulted in an increase in the shoot dry mass of red leaf lettuce (*Lactuca sativa*) 'Red Salad Bowl' from 3.0 to 10.0 g (Paz et al., 2019). Additionally, the total chlorophyll and carotenoid concentrations in leaf tissues increased by 42 and 57% respectively (Paz et al., 2019). Paz et al. (2019), similarly, found that as DLI increased from 2.2 to 9.7 mol·m^{-2}·d^{-1} anthocyanin concentration increased 16-fold. However, for shade-plants, an increasing DLI above 15 mol·m^{-2}·d^{-1} did not result in an increase in total dry mass for wax begonia (*Begonia ×semperflorens-cultorum*) 'Vodka Cocktail' or bedding impatiens (*Impatiens walleriana*) 'Cajun Red' (Faust et al., 2005). Orchidaceae is a family of plants in which species growth optimizes at high or low radiation intensity. Additionally, some orchids such as *Phalaenopsis* have been shown to preform CAM photosynthesis (Kubota et al., 1997). Optimum and maximum radiation intensities have been established for several commercially important genera of orchids. Lopez and Runkle (2005) reported a maximum radiation intensity of 300–600 µmol·m^{-2}·s^{-1} for *Cattleya*, 240–400 µmol·m^{-2}·s^{-1} for *Phalaenopsis*, and 300–500 µmol·m^{-2}·s^{-1} for *Zygopetalum*. In CAM plants, the difference between the maximum and minimum concentration of malic acid increases with an increasing DLI to a species-specific point (Kluge and Ting, 1978). However, as described above, the carbon fixation process in CAM plants can be different than in C_3 and C_4 plants.

For most plants, plant quality generally decreases under lower radiation intensities or certain radiation qualities (Armitage, 1991; Ilić and Fallik, 2017). High quality floriculture crops are typically defined as compact, well-branched, free of pests and diseases, colorful or variegated foliage, and may have an abundance or absence of flowers (Runkle, 2011). For instance, Faust et al. (2005) reported that time to flower of vinca (*Catharanthus roseus*) ‘Pacific Lilac’ and zinnia (*Zinnia elegans*) ‘Dreamland Rose’ increased by 9 and 3 d, respectively, when the radiation intensity was reduced from a moderate DLI of 11.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ to a low DLI of 4.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Flower number of bedding impatiens ‘Cajun Red’ was approximately half for plants grown under low DLIs, compared to those grown under moderate DLIs (Faust et al., 2005). Niu et al. (2001) reported that stem diameter of campanula (*Campanula carpatica*) ‘Blue Clips’ increased by 4 mm as DLI increased from 4.2 to 10.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$.

Some research investigating the impacts of radiation intensity exists for succulents. For instance, under low DLIs the growth rate of Christmas cactus (*Schlumbergera ×buckleyi*) is negatively impacted. As peak radiation intensity decreased from 759 to 185 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, stem number and dry mass decreased by 15 and 3.4 g per plant, respectively (Spurway and Thomas, 1992). Some work has been done with *Kalanchoe* suggesting that higher DLIs impact plant quality and development. Time to first open flower for *Kalanchoe laciniata*, *K. manginii*, and *K. velutina* decreased by 12, 11, and 14 d, respectively, as DLI increased from 4.3 to 17.2 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Currey and Erwin, 2011a).

In contrast, Khaimov and Mizrahi (2006) found that, with both red dragon fruit (*Hylocereus undatus*) and yellow dragon fruit (*Selenicereus megalanthus*), adding 60% shade resulted in the greatest number of fruit-forming flowers for both species. However, the authors did not report the DLI for the experiment, so it is difficult to know how radiation resulted in decreased reproductive vigor. To our knowledge, no research has been done on the interaction of DLI and temperature on growth and development of succulents.

Temperature

Mean daily temperature (MDT) is the main driver of plant development. Plant development is the process by which a plant moves through the various stages of its lifecycle, with the ultimate goal of reproduction. Generally, the rate of plant development follows an exponential curve as a function of temperature (Abrol and Ingram, 1996). The base temperature (T_b) is the temperature at or below which development cannot occur; as temperature increases above T_b, development increases until the optimum temperature T_{opt} is reached, at which development is maximal (Blanchard and Runkle, 2011). Above the T_{opt}, development decreases until the maximum temperature (T_{max}) is reached, where the development ceases (Blanchard and Runkle, 2011). However, T_{opt}, T_b, and T_{max} are species-dependent; plants native to different environments may have evolved tolerance to different temperatures. For example, smooth orache (*Atriplex glabriuscula*), a plant native to cool coastal environments, has a T_{opt} near 25 °C while Arizona honeysweet (*Tidestromia oblongifolia*), a plant native to the desert, has a T_{opt} near 45 °C (Berry and Bjőrkman, 1980). While MDT is important to plant development, temperature during the day and night periods can also have an impact on plant growth and development. High night temperatures above 30 °C have been shown to impact germination rates and growth of soybean (*Glycine max*) (Gibson and Mullen, 1996). Similarly, rice (*Oruza sativa*) yields can decline by as much as 10% for every 1 °C increase in night temperatures over the course of a season (Peng et al., 2004).

The effect of temperature on succulent growth and development have been observed in several key genera. For example, Erwin et al. (2017) found that leaf unfolding rate increased for mescal agave (*Agave parryitruncata*), aloe (*Aloe hybrida*) 'Firebird', Mexican hens and chicks (*Echeveria subsessilis*), zebra plant (*Haworthia fasciata*), prostrate rainbow bush (*Portulacaria afra variegata*), and burro's tail (*Sedum burrito*) when the MDT increased from 10 to 22 °C. However, the leaf unfolding rate of tree houseleek (*Aeonium percarneum*) 'Kiwi' decreased and burro's tail, tree houseleek 'Sir William Lawrence', and jade (*Crassula arborescens*) 'Silver Dollar' died as the MDT increased from 22 to 28 °C (Erwin et al., 2017). Leaf unfolding rate of lithops (*Lithops* spp.), Mexican hens and chicks (*Echeveria hybrida*) 'Lola', and gasteraloe (*Gasteraloe hybrida*) 'Green Ice' was not impacted as MDT increased from 10 to 22 °C (Erwin et al., 2017). This study demonstrates there are species-specific responses to temperature among succulents, and crops should be categorized by optimum temperatures for greenhouse production. In addition, Erwin et al. (2017) dispelled the misconception that all succulents require high temperatures for optimal growth. To our knowledge, few, if any, studies have been conducted to determine the T_b, T_{opt}, and T_{max} on the responses of CAM plants to MDT. Larsen et al. (1998) grew Thanksgiving cactus (*Schlumbergera truncata*) at a range of temperatures and found that plants flowered 43 and 113 d, after the start of short photoperiods at 24 and 12 ºC, respectively. However, plants were not grown at temperatures above 24 °C.

Additionally, the difference between the day and the night temperature (DIF) can have a profound effect on plant morphology. When taken together, night temperature and DIF can impact height, internode length, branching pattern and orientation, and flower stalk elongation in plants (Myster and Moe, 1995). DIF can be used on crops with poor affinity, incompatibility with chemical growth regulation, or non-labelled crops such as vegetable and herb transplants.

Erwin (1992) found that for the vegetable crops tomato (*Solanum lycopersicum*), sweet corn (*Zea mays*), and watermelon (*Citrullus lanatus*), internode length decreased by 68, 68, and 80%, respectively, as DIF increased 12 °C. However, development rates have been shown to be impeded by highly negative DIFs on poinsettia (*Euphorbia pulcherrima*) (Myster and Moe, 1995).

Plant Growth Regulators

For most floriculture crops, desirable characteristics in commercial crop production include compact growth, rapid, uniform, and complete flowering, and low pest pressure (Roh and Lawson, 1998), while for consumers, it is attractive, low-maintenance plants that do not deteriorate. Manipulation of greenhouse environmental conditions such as photoperiod, radiation intensity, and temperature can influence plant morphology, as described in the sections above. However, there are other methods by which excessive stem elongation can be regulated, including the use of synthetically derived plant growth regulators (PGRs).

One of the most popular classes of PGRs are those that inhibit gibberellin biosynthesis, which, in effect, reduces or prevents cell elongation and division depending on the active ingredient and concentration (Megersa et al., 2018; Rademacher, 1991). This class of PGRs includes chemicals such as pyrimidines, 4-pyridines, and triazoles, which each inhibit gibberellin production at different steps of the biosynthesis pathway (Grossmann, 1992). These classes of chemicals provide the floriculture industry with flexibility in production systems. However, excessive use of PGRs has been shown to be detrimental to plant growth, with some classes of growth regulators used as commercial herbicides (Anderson, 2005). PGR overdose can also occur, causing stunted plant growth for longer than the intended time period (Runkle, 2006).

Phytotoxicity, leaf curling and yellowing, delayed flowering and distorted growth can all be potential side effects of excessive PGR application (Whipker et al., 2001).

PGRs, such as paclobutrazol and uniconazole, have been used effectively during the cutting stage to inhibit stem elongation of finished *Kalanchoe* 'Rako' and 'Gold Strike' (Hwang et al., 2008). Some work has also been done on *Kalanchoe* involving spray applications on rooted plants. Currey and Erwin (2012) reported that applications of paclobutrazol and uniconazole are effective because of their ability to be absorbed despite the thick waxy cuticle. The effects of paclobutrazol on mature yellow dragon fruit suggest that paclobutrazol can be used to increase flower yield by up to 41% with no change in time to flower (Khaimov and Mizrahi, 2006).

A second important class of PGRs are synthetic gibberellins and cytokinins, which work to promote stem elongation and promote or inhibit flowering of some plants (Rodrigues et al., 2012). Gibberellic acid (GA_3) and benzyladenine (BA), a gibberellin and cytokinin, respectively, have been shown to increase offsets, leaf length, and leaf number in aloe vera (*Aloe barbadensis*) at rates of 400 $mg \cdot L^{-1}$ (Sardoei, 2014). This has been substantiated by Carey et al. (2008) in their work on *Echeveria* and *Sempervivum*, where they found *Sempervivum* offset number increased by 222% and *Echeveria* produced 700% more flower stalks as BA rate increased from 0 to 400 $mg \cdot L^{-1}$. In Easter cactus (*Rhipsalidopsis gaertneri*), BA had the benefit of increasing the number of total flower buds while only delaying flowering by as much as 3 d (Boyle, 1995).

Indoor radiation intensities can be reduced as much as 99% when compared to outdoor radiation intensities (Giorgioni and Neretti, 2009). Some studies investigating the impacts of the indoor radiation environment on plant growth and development have used DLIs as low as 0.16 $mol \cdot m^{-2} \cdot d^{-1}$ and as high as 7.8 $mol \cdot m^{-2} \cdot d^{-1}$ (Kim et al., 2012; Kubatsch et al., 2007). Under low

DLIs, plant photosynthesis can be greatly reduced, and internode elongation can occur, resulting in low plant quality. To our knowledge, no one has investigated if high substrate PGR drench rates under low radiation conditions can prevent excessive extension growth of succulents. This work could be beneficial to consumers by increasing the life span of houseplants grown under low radiation conditions, and to growers by providing a crop with a longer shelf life.

Environmental factors such as radiation and temperature often interact to affect plant growth and development. Often manipulation of one environmental variable does not give context to how a species would respond to changes to other environmental parameters. Therefore, research is needed investigating the effects of changes to multiple environmental parameters simultaneously to give greater context to changes in plant physiology. Understanding how succulents respond to radiation duration and intensity and temperature could result in a better understanding of these unique plants and increase grower profitability.

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SECTION II

Short day lengths can prevent excessive stem elongation and promote flowering of some *Echeveria* cultivars under low and moderate daily light integrals

Anthony J. Soster and Roberto G. Lopez*

Department of Horticulture, 1066 Bogue Street, Michigan State University, East Lansing, MI 48824-1325, USA

*Corresponding author. Tel.: +1 517-353-0342. E-mail address: rglopez@msu.edu (R.G. Lopez).

Abstract

Mexican hens and chicks (*Echeveria* spp.) are one of the most popular genera sold as they are compact with symmetrical rosettes containing brightly colored, fleshy, and broad iridescent leaves and large and showy inflorescences. However, they are very slow growing and flower induction protocols are lacking. Therefore, the objectives of this study were 1) to establish the critical photoperiod for flower induction of several cultivars of *Echeveria*; and 2) to determine if photoperiod and the photosynthetic daily light integral (DLI) can be manipulated to promote rapid growth and leaf expansion without excessive stem elongation. Cuttings of *E.* spp. and hybrids 'Apus', 'Canadian', 'Elegans Blue', 'Jade Point', and 'Topsy Turvy' were received from a commercial breeder and grown in a greenhouse at 20 °C for 5 weeks. Photoperiods were created using a truncated 9-h short day (SD) or a SD extended to 10, 11, 13, 15, 16-h or a 4-h night-interruption (NI), using light-emitting diode (LED) lamps providing a total photon flux density (TPFD) of ≈2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ of red (R) + white (W) + far-red (FR) radiation. DLIs of 4.8 and 12.8 $mol \cdot m^{-2} \cdot d^{-1}$ were created with and without shade cloth and supplemental lighting. Photoperiod and DLI interacted to influence final height of *E.* 'Canadian', 'Elegans Blue', and 'Jade Point'; plants were tallest under photoperiods >13-h and a low DLI. Similar trends were observed for growth index and average plant diameter indicating that longer photoperiods and lower DLIs resulted in larger plants, although aesthetic quality deteriorated under these environmental conditions. No clear trend was observed for leaf unfolding or leaf length across DLIs or photoperiods. Flower initiation of *E.* 'Apus' and 'Jade Point' was highest under a moderate DLI of 12.8 $mol \cdot m^{-2} \cdot d^{-1}$. Additionally, *E.* 'Jade Point' only developed inflorescences under day lengths ≤11 h, indicating an obligate SD response. Our results suggest growers should maintain DLIs >10 $mol \cdot m^{-2} \cdot d^{-1}$ and SD conditions if they want to promote flower initiation of some *Echeveria* cultivars and prevent excessive stem elongation. Under low and moderate DLIs, day-extension (DE) or NI lighting providing R + W + FR radiation was not beneficial at promoting leaf expansion, plant diameter or reducing time to produce a high-quality and marketable plant.

Keywords: Crassulaceae, DLI, Mexican hens and chicks, potted plants, succulents

Abbreviations: CAM, Crassulacean acid metabolism; CO_2, carbon dioxide; DE, day-extension; DLI, daily light integral; FR, far-red; HPS, high-pressure sodium; *PPFD*, photosynthetic photon flux density; LED, light-emitting diode; MDT, mean daily temperature; NI, night-interruption; P_{FR}, phytochrome far-red; P_{R}, phytochrome red; RO, reverse osmosis; SD, short day; TPFD, total photon flux density; U.S., United States

Introduction

Potted succulent sales continue to increase due to their unique appearance, diversity, adaptability, drought tolerance, ease of maintenance, new varieties, colors, and forms being introduced into the market (Armitage, 2016; Machovina, 2017; Wright, 2015). Their wholesale value over the past twenty years has increased by over 333% (USDA, 1998; 2019). However, unlike most other ornamental plants, succulents require unique growing conditions as they are xerophytes that are adapted to living in arid environments with limited water availability (Das and Panda, 1995). For this reason, it is difficult to propagate and produce them outdoors in northern latitudes, making them highly suitable for greenhouse production and indoor environments. However, little scientific production information is available on this diverse group of plants.

While some succulent genera are native to equatorial regions, others are found in northern and southern latitudes (Erwin et al., 2017). The vast majority come from the stonecrop family Crassulaceae and include the following genera: Tree house leek (*Aeonium*), round-leafed navel-wort (*Cotyledon*), jade plant (*Crassula*), Mexican hens and chicks (*Echeveria*), kalanchoe (*Kalanchoe*), jewel plant (*Pachyveria*), stonecrop (*Sedum*), and houseleek (*Sempervivum*). Mexican hens and chicks (*Echeveria*) is one of the most popular hybridized succulent genera sold in the United States (U.S.). There are more than 125 species and hybrids of *Echeveria* that are produced as potted plants (Uhl, 1992). *Echeveria* is slow growing and can take as long as 4 to 6 months to become a marketable plant from an unrooted cutting (Anonymous, 2007). Their native range extends from the southwestern U.S. into Mexico and southward into the highlands of Central and South America (Uhl, 1992). They are pioneer plants that colonize new habitats after volcanic activity and grow on rocky cliffs and lava escarpments (Guillermo et al., 2019).

Succulents are generally considered to use CAM exclusively as their primary means of photosynthesis, and this may be the case for nearly all species in the Crassulaceae family (Ting, 1985). However, suggesting that all succulents use CAM exclusively is an oversimplification (Ranson and Thomas, 1960). In general, CAM photosynthesis is considered an adaptation to arid climates with dry, hot days and relatively cool nights. However, succulents can be found in humid regions where they are restricted to microhabitats where low soil moisture reduces competition from other native plants (Medina and Delgado, 1976). Recent research suggests that CAM photosynthesis, in some species, is a facultative trait present under drought conditions and absent under the rainy season or wet conditions (Holtum et al., 2017; Winter and Holtum, 2017;

von Willert et al., 1985). Additionally, some work has been conducted investigating the impact of photoperiod on facultative CAM photosynthesis. For example, *Kalanchoe blossfeldiana* 'Tom Thumb' and *K. velutina* both exhibited an increase in the rate of CAM metabolites under short-days (SD) conditions (Brulfert et al., 1982). This effect is most pronounced in malate concentration; *K. blossfeldiana* grown under short-day (SD) conditions contained malate concentrations above 1.5 $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{dw}$, while plants grown under long day (LD) conditions had malate concentrations near zero (Brulfert et al., 1982).

Changes in day length can initiate developmental processes in day length-sensitive plants. These plants utilize photoreceptors such as phytochromes and cryptochromes to sense the length of the night period, resulting in a promotion or a suppression of flowering (Lin, 2000). Phytochrome has two interconvertible isometric forms P_{FR} and P_R, which can be converted based on the relative abundance of red (R) or far-red (FR) radiation (Lin, 2000). Day-extension (DE) or night-interruption (NI) lighting containing R and FR radiation is often used to induct LDPs into flower, as the accumulation of P_{FR} initiates a flowering response (Runkle and Heins, 2001). In certain plants, the shade avoidance response is also initiated when plants are exposed to high proportions of FR radiation, causing elongation of stems and petioles (Ruberti, et al., 2012).

Burlfert et al. (1975), further discuss the implications of facultative CAM as a phytochrome-mediated response, suggesting the parallel between CAM induction and flower initiation are mediated by the same molecular mechanisms. However, early photoperiod studies with *K. blossfeldiana*, were often conducted under high-intensity NI lighting from fluorescent lamps that provided R radiation (Brulfert et al., 1973; 1975; 1982; Queiroz and Morel, 1974). Despite the fact that these fixtures did not provide FR radiation, plants exhibited metabolite rhythms characteristic of CAM photosynthesis; an increase in malate and PEP carboxylase.

Therefore, research investigating the effects of low-intensity photoperiod lighting providing R and FR radiation and the implications of phytochrome as the mechanism for CAM plant growth and development are needed.

Since many succulents are slow growing, there is interest in investigating how environmental conditions such as photoperiod and the daily light integral (DLI) can be manipulated to promote rapid vegetative growth and flowering (Erwin, 2009). For example, Calle et al. (2010), carried out an observational study where cacti and succulents native to South Africa were observed in conservatories over time at latitudes ranging from 0 to 48 °N. They documented most cacti and succulents had flowers during the shortest day lengths of the year. Similarly, Currey and Erwin (2011b) reported that *Kalanchoe* species native to South Africa and Madagascar differed in their responses to photoperiod. For example, *K. glaucescens*, *laciniata*, *manginii*, *nyikae*, *rotundifolia*, *uniflora*, and *velutina* were classified as obligate SD plants, while *K. beauvardii*, *behariensis*, *fedtschenkoi*, *longifloria*, *marmorata*, *marnieriana*, *streptantha*, *tomentosa*, and *vigueridoi* had seemingly no response to day length. In a separate study, as day length increased from 6 to 18-h, the number of new prickly pear cactus (*Opuntia ficus-indica*) cladodes (water-storing stems) increased from one to over four (Nobel, 1989), suggesting photoperiod may influence growth as well as development.

Work by Buchanan-Bollig (1984) also suggests that increasing radiation intensity results in increased carbon dioxide (CO_2) accumulation and starch production in *Kalanchoe blossfeldiana* at different photoperiods. During a constant 24-h dark period, net CO_2 uptake and transpiration was negative while during a constant 24-h light period, CO_2 uptake oscillated depending on the radiation intensity, with more extreme peaks and troughs occurring at lower radiation intensities (Buchanan-Bollig, 1984). Currey and Erwin (2011a) also investigated the effects of DLI on several species of *Kalanchoe* and they indicated that dry mass of *K. glaucescens*, *laciniata*, *manginii*, *nyikae*, *rotundifolia*, and *velutina* increased as the DLI increased from 4.3 to 17.2 mol·m^{-2}·d^{-1}. Similarly, the dry mass of Christmas cactus (*Schlumbergera ×buckleyi*) increased by 8.5 g as shade was reduced from 75% to 0% during the production cycle (Spurway and Thomas, 1992). Cabahug et al. (2017) reported that stem elongation of *Echeveria marcus* and *E. agavoides* was reduced from 47.0 to 41.6 mm and 44.8 to 42.0 mm, respectively, as the DLI increased from 1.7 to 6.8 mol·m^{-2}·d^{-1}.

Some studies have also documented the interaction of DLI and photoperiod on cacti and succulents. Nam et al. (2016) determined that height of *Sedeveria* 'Letizia' increased under light emitting diode (LED) fixtures providing 3 h of DE lighting. For example, at radiation intensities of 60 and 120 µmol·m^{-2}·s^{-1} height was 60.7 and 68.4 mm, respectively (Nam et al., 2016). However, it was not possible to isolate the main effects of photoperiod and radiation intensity on plant growth as a low-intensity DE treatment was not utilized.

To our knowledge, few if any studies investigating the effects of DLI and a range of photoperiods on *Echeveria* growth and development have been published. For these reasons, the objectives of our study were to 1) establish the critical photoperiod for flower induction of cultivars of *Echeveria*; and 2) to determine if photoperiod and the DLI can be used to hasten production without excessive stem elongation.

Materials and Methods

Cuttings of Mexican hens and chicks (*Echeveria* spp.) 'Apus', 'Canadian', 'Elegans Blue', 'Jade Point', and 'Topsy Turvy' were received from a commercial breeder (Dümmen Orange, Columbus, OH) on 29 Apr., 19 May, and 27 May 2020. One day after receipt, cuttings were inserted into 11-cm-diameter round containers (600-mL) (East Jordan Plastics Inc., East Jordan, MI) filled with 75% (by vol.) commercial soilless media, composed of 70% peat moss, 21% perlite, and 9% vermiculite (Suremix; Michigan Grower Products Inc., Galesburg, MI), and 25% perlite (Coarse Perlite; Perlite Vermiculite Packaging Industries Inc., North Bloomfield, OH). A foliar spray containing indole-3-butyric acid (Advocate; Fine Americas, Inc., Walnut Creek, CA) and a surfactant (Capsil; Aquatrols, Paulsboro, NJ) was applied at a concentration of 75 $\text{mg}\cdot\text{L}^{-1}$ and volume of 0.2 $\text{L}\cdot\text{m}^{-2}$ one day after transplant.

The cuttings were rooted in a glass-glazed greenhouse at Michigan State University (East Lansing, MI; lat. 43° N). An environmental control computer (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada) controlled evaporative cooling, radiant hot-water heating, exhaust fans, and supplemental lighting. A 16-h photoperiod was maintained with high-pressure sodium lamps (LR48877; P.L. Lighting, Beamsville, ON, Canada) that provided a total photon flux density (TPFD) of 62.5 ± 2.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The DLI and mean daily temperature (MDT) during propagation were 19.4 ± 4.6 and 18.7 ± 2.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, and 22.7 ± 2.4 and 22.7 ± 2.2 °C, respectively for replications (Reps.) 1 and 2. Plants were irrigated as needed with reverse osmosis (RO) water blended with a water-soluble fertilizer (MSU Orchid RO Water Special 13N–1.3P–12.5K; Greencare Fertilizers, Inc. , Kankakee, IL) containing ($\text{mg}\cdot\text{L}^{-1}$): 125 N, 13 P, 121 K, 78 Ca, 19 Mg, 0.17 B, 0.43 Cu, 1.7 Fe, 0.85 Mn, 0.17 Mo, and 0.43 Zn.

After 44 d, plants were transferred to one of 16 benches in a separate glass-glazed greenhouse. Opaque black cloth was pulled over each individual bench at 1700 HR and was retracted at 0800 HR to create a truncated 9-h SD. The photoperiod consisted of natural day lengths and supplemental lighting from 200-W LED fixtures (Philips GP-TOPlight DRW-MB;

Koninklijke Philips N.V., Eindhoven, the Netherlands) that provided 78 ± 20 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$ when the outdoor light intensity was below ≈440 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$. The 100-nm waveband ratios (%) of the LED fixtures, defined by their blue [B (400-500 nm)], green [G (500-600 nm)], and red [R (600-700 nm)] photon flux densities (PFD) was 10:5:85. On each bench four R + white (W) + far-red (FR) LED lamps (Arize™ Greenhouse Pro; General Electric, Boston, MA) were used to create 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h NI from 2200 to 0200 HR. The lamps were covered with an aluminum mesh to reduce the TPFD to ≈2 $\mu\mathrm{mol}\cdot\mathrm{m}^{-2}\cdot\mathrm{s}^{-1}$. The 100-nm waveband ratios (%) of the lamps were 6:19:45:30 as defined by the B, G, R and FR PFD, respectively. Two different DLIs were created using shade cloth placed over individual benches that reduced radiation levels by ≈60% (Harmony 5120 O E; Ludvig Svensson, Kinna, Sweden) or no shade. The MDT and mean DLI ± SD are provided in Table 1.

At transplant, initial plant height from the base of the plant to the tallest point on the plant, plant diameter at the widest point and perpendicular from the widest point, and the total number of leaves were measured and recorded. After 10 weeks under treatments, final length of the oldest leaf, number of newly unfolded leaves, node and branch number, plant height from the base of the plant to the tallest point on the plant, plant diameter at the widest point and perpendicular from the widest point were measured and recorded. Stem caliper was measured from just above the medium using a digital caliper (41101 DigiMax; Wiha, Buchs, Switzerland). Growth index was calculated (GI = {plant height + [(diameter 1 + diameter 2)/2]}/2) (Krug et al., 2010). Plants were designated as reproductive or non-reproductive depending on the presence or absence of an inflorescence, and number of inflorescences per plant were recorded. Total shoot (leaves and stems) fresh mass was quantified using a digital balance, afterwards shoots were placed in a drying oven at ≥70 °C for ≥7 d to determine the dry mass. The experiment was organized in a randomized complete-block design with a two-way factorial arrangement. Plants were blocked by photoperiod (seven levels) and DLI (two levels) with 10 randomly selected plants per treatment combination. The experiment was performed twice over time for the five cultivars evaluated. Data were analyzed separately by cultivar, and cultivar interaction was not evaluated. Data were analyzed with SAS version 9.4 (SAS Institute, Inc., Cary, NC) mixed model procedure (PROC MIXED) for analysis of variance (ANOVA). Means were separated using the Tukey-Kramer honestly significant difference test ($P \leq 0.05$).

Results

The DLI and photoperiod interacted to influence the final height of *E.* ‘Canadian’, ‘Elegans Blue’, ‘Jade Point’, and ‘Topsy Turvy’, but not *E.* ‘Apus’. However, no clear trend was present for ‘Topsy Turvy’. The tallest plants were those under 15- or 16-h photoperiods and a low DLI of 4.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 2; Fig. 1). Under a low DLI, *E*. ‘Elegans Blue’ was 11%, 8%, 11%, 26%, 28%, 20%, and 29% taller under a 9-, 10-, 11-, 13-, 15-, 16-h photoperiod or a 4-h NI, respectively, than under a moderate DLI (Fig. 1). Individually, photoperiod and DLI influenced the height of *E.* ‘Apus’; however, no trends existed (Tables 3 and 4).

Similar to final height, growth index of *E*. ‘Canadian’, ‘Elegans Blue’ and ‘Jade Point’ was influenced by the interaction of DLI and photoperiod; resulting in larger plants under longer photoperiods and lower DLIs (Table 2; Fig. 2). The largest *E*. ‘Canadian’, ‘Elegans Blue’, and ‘Jade Point’ were generally those grown under long photoperiods and low DLIs (Fig. 2). Growth index of *E*. ‘Topsy Turvy’ was not influenced by photoperiod or DLI (Table 2).

E. ‘Jade Point’ was the only cultivar whose diameter was influenced by the interaction of DLI and photoperiod, but no clear trend was discernable (Table 2, Fig. 3). However, individually

DLI and photoperiod influenced the diameter of *E*. ‘Apus’, ‘Jade Point’, and ‘Elegans Blue’ (Table 2). As the DLI increased from 4.6 to 12.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ the average diameter of *E*. ‘Apus’, ‘Jade Point’, and ‘Elegans Blue’ increased by 1.4, 0.4, and 1.3 cm, respectively (Table 4).

Although leaf unfolding was influenced by the interaction between DLI and photoperiod for *E*. ‘Topsy Turvy’, no trend was observed (Fig. 4). Generally, leaf unfolding responses to the two environmental parameters were cultivar specific. For example, *E*. ‘Apus’ was not influenced by either DLI or photoperiod, whereas *E*. ‘Elegans Blue’ was only influenced by photoperiod with the highest leaf unfolding occurring under photoperiods ≥13-h (Table 2). Under a 13-h photoperiod, plants unfolded 2.7 and 1.5 more leaves than those plants grown under a 9-h or 16-h photoperiod, respectively (Table 3). Few differences were observed in leaf unfolding of *E*. ‘Canadian’ and ‘Topsy Turvy’ (Fig. 4). However, *E*. ‘Jade Point’ had the greatest number of leaves when photoperiods were ≥15-h or included a NI with a low DLI compared to all other treatments (Fig. 4).

No interaction between DLI and photoperiod was observed for leaf length or stem caliper for any cultivar (Table 2). Generally, DLI and photoperiod had minimal influence on leaf length (Tables 3 and 4). However, under a moderate DLI, stem caliper of *E*. ‘Canadian’, ‘Elegans Blue’, ‘Jade Point’ and ‘Topsy Turvy’ increased (Table 2). For instance, the stem caliper of *E*. ‘Canadian’, ‘Elegans Blue’, ‘Jade Point’, and ‘Topsy Turvy’ was 1.1, 0.6, 0.5, and 0.5 mm greater under the moderate DLI compared to the low DLI (Table 4).

DLI and photoperiod interacted to affect the dry mass of *E*. ‘Jade Point’, photoperiod influenced ‘Topsy Turvy’; however, no clear trends existed (Table 3; Fig. 3). Under a moderate DLI, dry mass of *E*. ‘Elegans Blue’ was 35% greater compared to plants grown under a low DLI (Table 4).

E. 'Canadian' developed the greatest number of inflorescences per plant under 15 and 16-h photoperiods; however, flowering occurred under all photoperiods (Table 3). *E*. 'Apus' developed 0.11 inflorescences per plant under a moderate DLI, compared to 0 inflorescences under a low DLI (Table 4). DLI and photoperiod interacted to influence inflorescence number of *E*. 'Jade Point', the most inflorescences were observed under a day length of 9-h and moderate DLI (Fig. 3). The percent of plants developing an inflorescence was cultivar specific. For example, the highest percentage of *E*. 'Apus', 'Elegans Blue', and 'Jade Point' developed inflorescences under photoperiods ≤11-h and a moderate DLI and no plants developed inflorescences at photoperiods ≥13-h (Fig. 5). In contrast, the highest percentage of *E*. 'Canadian' that developed an inflorescence occurred under a 15-h photoperiod and a low DLI. However, there was no clear trend for the percentage of 'Topsy Turvy' that developed an inflorescence (Fig. 5).

Discussion

This study was developed based on preliminary data indicating plant diameter of *Echeveria* was promoted under long photoperiods created with low-intensity LEDs providing R+W+FR radiation. In the preliminary study, *Echeveria* 'Domingo' was grown for 12 weeks under 9-, 12-, 14-, and 16-h photoperiods and a much higher DLI and MDT of 22.9 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and 26.7 °C, respectively. Interestingly, we found that plant diameter increased with increasing day lengths as *E*. 'Domingo' grown under a 9-h photoperiod had an average width of 17.3 cm, compared to 22.2 cm for plants grown under a 16-h photoperiod, and no excessive stem elongation occurred (data not shown). This led to our hypothesis that providing long day lengths with DE or NI lighting utilizing FR radiation would result in larger plants as the FR would lead to leaf expansion as discussed by Park and Runkle (2017). The preliminary results of our study differed substantially from the results considered in this manuscript, as it is possible that growing succulents under high DLIs results in extension growth of leaves without stem elongation, resulting in a larger plant and no loss in quality. Additionally, *E*. 'Domingo' may show different responses to photoperiod than the cultivars selected for the current study.

High ratios of FR radiation can lead to leaf expansion and stem elongation due to the shade avoidance response (Demotes-Mainard et al., 2016). Leaf expansion resulting from FR radiation can, in some cases, be beneficial and lead to a higher-quality plant or shorter production time. For example, Park and Runkle (2017) found that increasing FR radiation during geranium 'Pinto Premium Orange Bicolor' and snapdragon 'Trailing Candy Showers Yellow' seedling production resulted in increased leaf expansion and net carbon assimilation. This led to larger seedlings and hastened flowering of snapdragon. Similarly, Meng et al. (2019), found that replacing blue radiation in LED fixtures with green or FR radiation resulted in an increase in leaf expansion and shoot mass of lettuce 'Rex' and 'Rouxai' and kale 'Siberian'.

The majority of DLI studies have been conducted on traditional greenhouse crops and have reported that it influences a number of plant growth processes, including the accumulation of biomass, time to flower, stem elongation, and leaf expansion (Franklin and Whitelamb, 2005; Kelly et al., 2020; Munir et al., 2004). However, few studies have investigated the effects of DLI on succulents. Currey and Erwin (2011a) reported that dry mass accumulation of *K. glaucescens*, *laciniata*, *manginii*, *nykae*, *rotundifolia*, and *velutina* increased by 3.9, 10.5, 4.6, 7.4, 8.5, and 11.1 $\text{mg}\cdot\text{d}^{-1}$, respectively, as DLI increased from 4.3 to 17.2 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Our results found that dry mass of only *E*. 'Elegans Blue' increased with DLI from 4.6 to 12.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 4). However, we observed an increase in dry mass with increasing photoperiod for *E*. 'Apus', 'Jade

Point', and 'Topsy Turvy' (Table 3). Currey and Erwin (2011a) reported flower number increased as DLI increased for *K. glaucescens*, *laciniata*, *manginii*, *nykae*, *rotundifolia*, and *velutina* by 41, 32, 25, 26, 62, and 73 flowers, respectively. Our results agree, as we observed an increase in the number of inflorescences *E.* 'Apus' and 'Jade Point' produced under the moderate DLI (Table 4).

Plant height is generally influenced by DLI, day and night temperature, photoperiod, and the shade avoidance response. Cabahug et al. (2017) found that *Echeveria agavoides* were 7% taller when grown under a very low DLI of 1.7 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared to those grown under a low DLI of 6.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Similarly, *Echeveria marcus* grown under the same environmental conditions were 13% taller under the very low DLI (Cabahug et al., 2017). The diameter of *E. agavoides* and *marcus* was 15 and 5% larger, respectively, when grown under a DLI of 1.7 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared to plants grown under 6.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Cabahug et al., 2017). Our results agree, as *E*. 'Canadian' and 'Elegans Blue' grown under low DLIs were 9% and 25% taller, respectively, compared to plants under the high DLI (Table 4). Similarly, we found that the average width of 'Jade Point' grown under 4.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ was 15% greater (Fig. 3). However, a deterioration in plant quality was generally observed under low DLIs and photoperiods ≥13 h as internode elongation was excessive (Fig. 6). Our results provide evidence that low DLIs, in combination with DE lighting containing FR, contributed to excessive stem elongation for some *Echeveria* cultivars. Further research investigating the effect of DE lighting without FR radiation may provide greenhouse growers with information on how to successfully promote growth of succulents without excessive stem elongation.

For traditional floriculture crops, plant quality is a combination of branching, compactness, plant health, foliage filling in the container and some open flowers (Runkle, 2011).

However, plants that are sold solely for their unique foliage differ in their quality attributes. They must have attractive, brightly colored leaves that are favored over their flowers and fruits and perform well in any indoor environment (Chen et al., 2002). Similar to containerized flowering plants, they must also fill in the container, be compact, well branched in certain genera and be free of pest, diseases, and blemishes. Excessive stem elongation, or elongation to the point of low quality is often not tolerated. Additionally, flowers of some succulent genera are unsightly, and as a result may be unappealing to consumers. Recent research has been conducted to investigate how the promotion of foliage plant benefits can influence consumer purchasing behavior (Rihn et al., 2015). Investigators have also determined how visual cues and communication of essential information can influence likeliness to purchase (Khacatryan et al., 2018). However, research relating to consumer preferences for vegetative, flowering, and foliage color of succulents needs to be conducted in order to provide growers with information to further increase sales.

Horticulturally, rapid, uniform, and complete flowering is essential to meet market dates. However, little research has been performed outside of *Kalanchoe* spp. to determine the critical photoperiod for flower initiation of succulents. Although Calle et al. (2010) observed that many of the South-African succulents grown in public conservatories flowered under SD, they did not have large sample sizes. For *Kalanchoe* spp., Currey and Erwin (2011b) determined that many common species responded to day length as SDPs. However, they were not able to classify all species due to low flowering percentages. In the current study, only *E.* 'Jade Point' produced inflorescences under day lengths ≤11-h, thus we have classified it as an obligate SDP (Table 3). While we did not quantify time to flower, visually we observed inflorescence development of *E.* 'Topsy Turvy' was hastened under shorter day lengths, indicating that it may have a facultative

SD flowering response (Fig. 6). Although other cultivars in this study developed inflorescences, there was no consistent trend in response to day length, and flowering percentages were generally low.

Echeveria is one of the most easily hybridized genera of succulents, both within the genus and within genera in the Crassulaceae family (Uhl, 1992). Many commercially available cultivars have parents from different continents, latitudes, and elevations, resulting in an outpouring of genes from diverse environments (Uhl, 1992). The commercial use of hybrid *Echeveria* and the unavailability of parent-line information makes it difficult to determine which combinations of environmental parameters might contribute to flowering responses. We hypothesize that a long juvenile period may be a characteristic of CAM plants resulting in a lack of complete and uniform flowering.

This study has also provided important information for growers located in northern latitudes: if increasing the DLI with supplemental lighting is not possible, a grower may still be able to reduce excessive stem elongation and improve quality. Photoperiodic lighting containing FR radiation should not be utilized when DLIs $\leq 10\ \mathrm{mol \cdot m^{-2} \cdot d^{-1}}$, as excessive internode elongation will lead to low quality plants. Given that some *Echeveria* cultivars appear to have a SD flowering response, DE or NI lighting containing R+W radiation would prevent premature flowering. To initiate flowering and produce the most compact plant, the day length could be shortened to <13 h. The low percentage of plants that flowered in this study indicate there may be additional mechanisms that influence flower initiation of *Echeveria*. More research is needed investigating the effects of high DLIs, R radiation, temperature, photoperiod, and juvenility on growth and development of potted succulents. Future experiments focusing on juvenility, dual photoperiods or vernalization requirements prior to placement under various photoperiods may provide useful data on how to induce rapid, complete, and uniform flowering of succulents. Lastly, studies focusing on consumer preference for flowering or non-flowering succulents and color preference would provide insight into the potential marketability of flowering succulents.

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APPENDIX

Table I-1. DLI, photoperiod (h), bench mean daily temperature (MDT) (±SD) and daily light integral (DLI) (±SD) during two experimental replications (Rep.). *Echeveria* were grown under a truncated 9-h short day (SD) or under a 9-h SD extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h night-interruption (NI).

DLI	Photoperiod (h)	Rep. 1 MDT [mean ± SD (°C)]	Rep. 2 MDT [mean ± SD (°C)]	Rep. 1 DLI ($mol\cdot m^{-2}\cdot d^{-1}$)	Rep. 2 DLI ($mol\cdot m^{-2}\cdot d^{-1}$)
Moderate	9	24.5 ± 1.8	24.6 ± 1.7	12.9 ± 4.5	12.5 ± 4.9
	10	23.8 ± 1.7	23.9 ± 1.5	-^{z}	-^{z}
	11	24.2 ± 2.3	24.2 ± 2.0	-^{z}	-^{z}
	13	24.9 ± 1.8	23.0 ± 1.7	12.8 ± 4.1	12.6 ± 4.5
	15	23.9 ± 1.9^{y}	24.2 ± 1.9^{y}	-^{z}	-^{z}
	16	23.8 ± 2.2	24.9 ± 2.2	12.7 ± 4.0	12.4 ± 4.3
	NI	23.8 ± 1.8	23.1 ± 1.7	12.9 ± 4.6	13.2 ± 4.7
Low	9	24.5 ± 2.1^{y}	24.7 ± 2.2^{y}	-^{z}	-^{z}
	10	23.6 ± 1.6	23.8 ± 1.6	4.2 ± 2.9	4.2 ± 3.1
	11	23.8 ± 1.8	24.0 ± 1.7	4.9 ± 1.5	5.0 ± 1.7
	13	23.6 ± 1.5	23.7 ± 1.5	4.2 ± 1.7	4.3 ± 1.9
	15	23.3 ± 1.5	23.4 ± 1.4	4.6 ± 2.6	4.8 ± 2.9
	16	24.3 ± 2.1	24.5 ± 2.0	4.4 ± 1.8	4.5 ± 2.0
	NI	23.4 ± 1.7	23.5 ± 1.6	4.7 ± 2.0	4.9 ± 2.2

^{y}Partial data reported

^{z}Data not reported

Table I-2. Analysis of variance for final height, average width, growth index, leaf unfolding, leaf length, stem caliper, dry mass, branch number and flower number of *Echeveria* grown under 9-, 10-, 11-, 13-, 15-, 16-h photoperiods (P) or a 4-h night interruption (NI) and low or moderate daily light integrals (DLI).

Parameter	P	DLI	DLI × P
		‘Apus’	
Final height	**^{z}	*	NS
Average width	**	***	NS
Growth index	**	***	NS
Leaf unfolding	NS	NS	NS
Leaf length	*	NS	NS
Stem caliper	NS	NS	NS
Dry mass	*	NS	NS
Branch number	NS	NS	NS
Flower number	NS	*	NS
		‘Canadian’	
Final height	***	***	***
Average width	NS	NS	NS
Growth index	***	NS	**
Leaf unfolding	***	NS	*
Leaf length	NS	NS	NS
Stem caliper	NS	***	NS
Dry mass	NS	NS	NS
Branch number	NS	*	NS
Flower number	**	NS	NS
		‘Elegans Blue’	
Final height	***	**	***
Average width	*	***	NS

Table I-2 (cont'd)

Growth index	***	***	***
Leaf unfolding	***	NS	NS
Leaf length	*	***	NS
Stem caliper	NS	***	NS
Dry mass	NS	*	NS
Branch number	NS	NS	NS
Flower number	NS	NS	NS
		'Jade Point'	
Final height	***	NS	**
Average width	***	*	**
Growth index	***	*	**
Leaf unfolding	***	***	**
Leaf length	*	*	NS
Stem caliper	NS	*	NS
Dry mass	*	NS	*
Branch number	NS	NS	NS
Flower number	**	**	*
		'Topsy Turvy'	
Final height	NS	NS	*
Average width	NS	NS	NS
Growth index	NS	NS	NS
Leaf unfolding	***	***	*
Leaf length	NS	NS	NS
Stem caliper	*	**	NS
Dry mass	*	NS	*
Branch number	NS	NS	NS
Flower number	NS	NS	NS

[z] NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

Table I- 3. Effect of 9-, 10-, 11-, 13-, 15-, 16-h photoperiod or a 4-h night interruption (NI) lighting on final height, average width, growth index, leaf unfolding, leaf length, stem caliper, dry mass, branch number, and flower number flower number of various *Echeveria* cultivars.

Parameter	Photoperiod (h)						
	9	10	11	13	15	16	NI
‘Apus’							
Final height (cm)	11.6 b	11.7 b	11.6 b	12.2 a	12.1 ab	11.9 ab	11.7 ab
Average width (cm)	10.4 b	10.8 ab	10.5 b	11.5 a	11.3 ab	10.6 b	10.5 b
Growth index	11.0 c	11.2 bc	11.1 bc	11.9 a	11.7 ab	11.2 bc	11.1 bc
Leaf length (cm)	5.7 b	6.0 ab	5.9 ab	6.5 a	6.3 ab	5.8 b	6.0 ab
Dry mass (g)	2.6 ab	2.7 ab	2.6 ab	2.8 a	2.7 a	2.4 b	2.6 ab
‘Canadian’							
Final height (cm)	11.9 b	12.0 b	12.2 b	13.1 a	13.6 a	13.4 a	12.3 b
Growth index	11.4 c	11.4 c	11.7 bc	12.3 ab	12.5 a	12.2 abc	11.6 bc
Leaf unfolding (no.)	35.6 a	34.9 a	35.0 a	34.6 ab	34.7 a	31.7 b	32.8 ab
Flower number (no.)	0.03 b	0.0 b	0.08 b	0.0 b	0.38 a	0.23 ab	0.03 b
‘Elegans Blue’							
Final height (cm)	14.3 c	14.8 c	15.2 c	20.1 b	22.2 a	21.6 a	19.4 b
Average width (cm)	7.7 ab	7.9 ab	7.6 b	8.1 a	8.1 ab	7.9 ab	8.1 ab
Growth index	11.0 c	11.4 c	11.4 c	14.0 b	15.1 a	14.7 a	13.7 b
Leaf unfolding (no.)	18.1 d	18.6 cd	18.0 d	20.8 a	20.3 ab	19.3 bcd	19.5 abc
‘Jade Point’							
Final height (cm)	11.4 c	11.9 abc	11.6 bc	12.1 a	12.1 a	12.2 ab	11.9 abc
Average width (cm)	8.7 b	9.3 ab	8.8 b	9.6 a	9.9 a	9.4 ab	9.2 ab
Growth index	10.1 c	10.6 ab	10.2 bc	10.9 a	11.0 a	10.8 ab	10.6 ab
Leaf unfolding (no.)	14.6 c	16.5 bc	14.6 c	17.5 b	22.3 a	19.0 b	19.0 b
‘Topsy Turvy’							
Stem caliper (mm)	13.2 c	12.9 ab	13.0 bc	13.8 abc	12.8 a	12.9 c	13.3 abc

Table I-3 (cont'd)

Leaf unfolding (no.)	32.7 ab	36.3 ab	33.5 ab	35.3 a	36.8 b	32.7 ab	34.9 ab

Table I-4. Effect of moderate or low daily light integrals (DLI) on final height, average width, growth index, leaf unfolding, leaf length, stem caliper, dry mass, branch number, and flower number of various *Echeveria* cultivars.

	DLI	
	Low	Moderate
	‘Apus’	
Final height (cm)	11.7 b	11.9 a
Average width (cm)	11.5 a	10.1 b
Growth index	11.6 a	11.0 b
Flower number (no.)	0.0 b	0.11 a
	‘Canadian’	
Final height (cm)	13.2 a	12.1 b
Stem caliper (mm)	10.2 b	11.3 a
Branch number (no.)	0.12 b	0.26 a
	‘Elegans Blue’	
Final height (cm)	20.3 a	16.2 b
Average width (cm)	8.1 a	7.7 b
Growth index	14.2 a	11.9 b
Leaf length (cm)	3.9 b	4.2 a
Stem caliper (mm)	6.6 b	7.2 a
Dry mass (g)	1.7 b	2.3 a
	‘Jade Point’	
Average width (cm)	9.9 a	8.6 b
Growth index	10.9 a	10.2 b
Leaf unfolding (no.)	19.2 a	15.7 b
Leaf length (cm)	4.5 b	4.7 a

Table I-4 (cont'd)

Stem caliper (mm)	7.8 b	8.3 a
	'Topsy Turvy'	
Stem caliper (mm)	12.9 b	13.4 a
Leaf unfolding (no.)	34.6 a	32.9 b

Figure I-1. Final height for *Echeveria* ‘Canadian’, ‘Elegans Blue’, and ‘Jade Point’ grown under a 9-h short day extended with red+white+far-red (R+W+FR) light-emitting diode (LED) lamps to achieve 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h night-interruption (NI) and under low or moderate daily light integrals (DLI). Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer honestly significant difference (HSD) test at $P \leq 0.05$. Bars represent the mean and error bars indicate standard error.

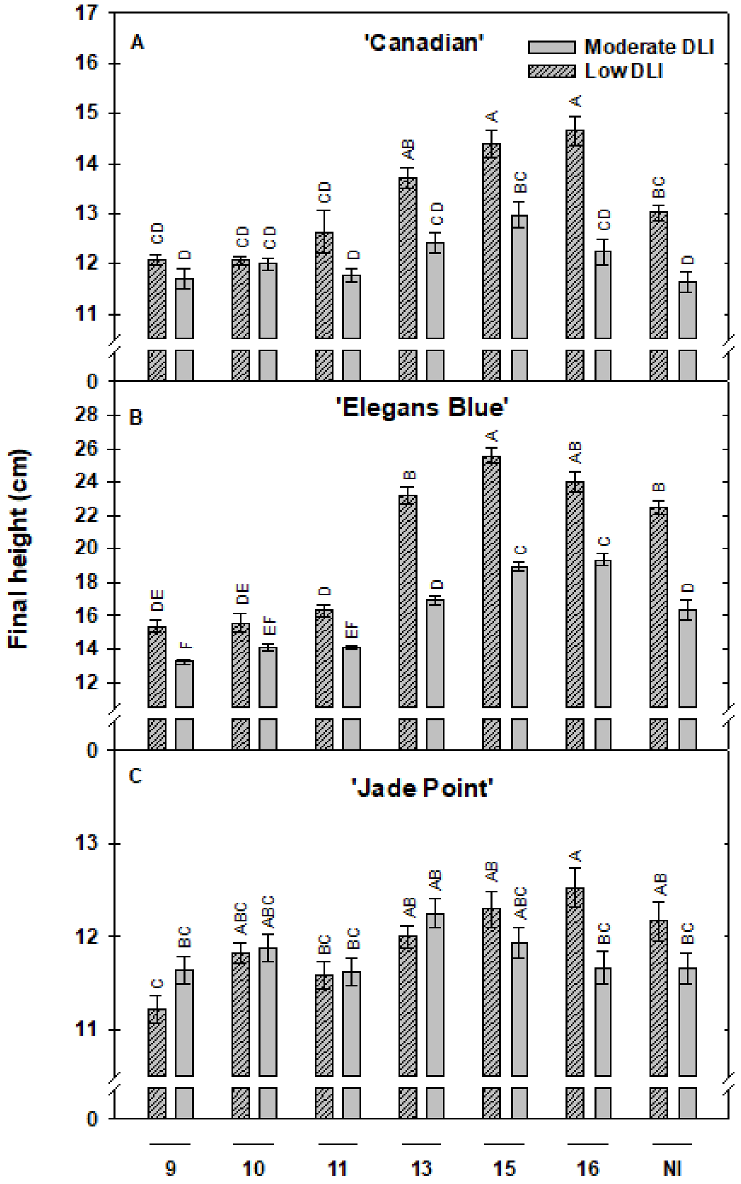


Figure I-2. Growth index for *Echeveria* ‘Canadian’, ‘Elegans Blue’, and ‘Jade Point’ grown under a 9-h short day extended with red+white+far-red (R+W+FR) LED lamps to achieve 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h night interruption (NI). Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer HSD test at P ≤ 0.05. Bars represent means and error bars indicate standard error.

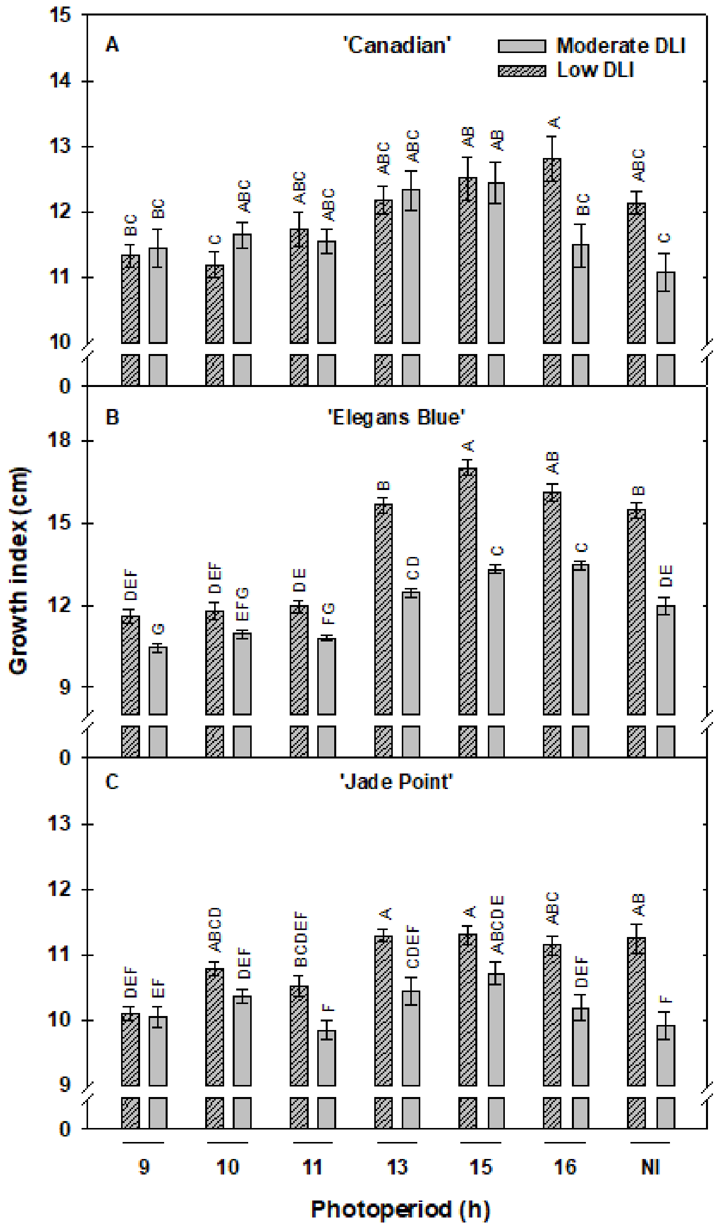


Figure I-3. Dry mass, average diameter, and flower number of *Echeveria* 'Jade Point' grown under 9-h short day extended with red+white+far-red (R+W+FR) LED lamps to achieve 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h night interruption (NI). Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer HSD test at P ≤ 0.05. Bars represent means and error bars indicate standard error.

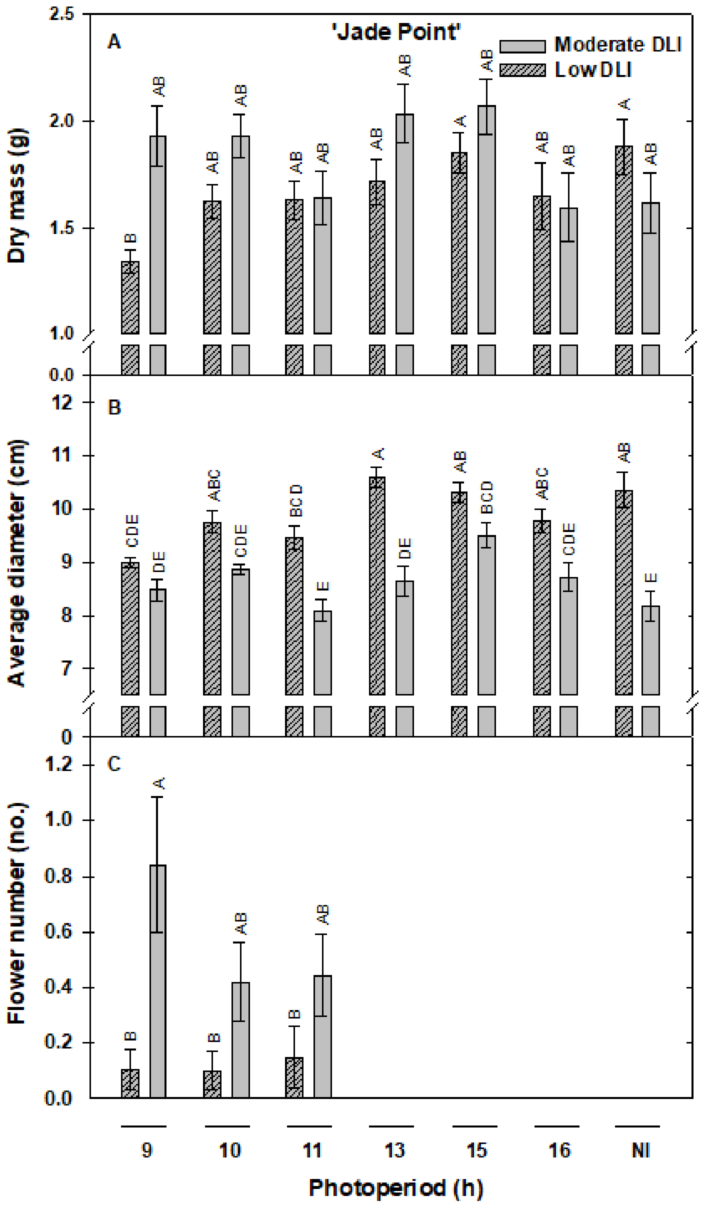


Figure I-4. Leaf unfolding of *Echeveria* ‘Canadian’, ‘Jade Point’, and ‘Topsy Turvy’ grown under 9-h short day extended with red+white+far-red (R+W+FR) LED lamps to achieve 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h night interruption (NI). Letters indicate mean separations across photoperiodic treatments using Tukey-Kramer HSD test at P ≤ 0.05. Bars represent means and error bars indicate standard error.

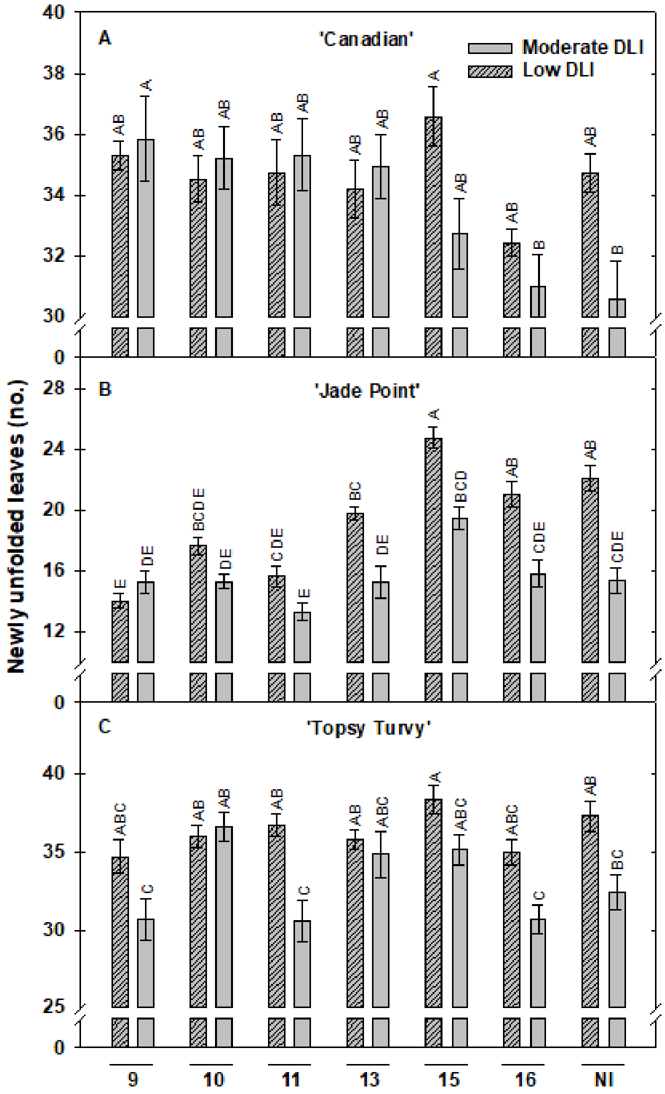


Figure I-5. Flowering percentage of *Echeveria* 'Apus', 'Canadian', 'Elegans Blue', 'Jade Point', and 'Topsy Turvy' grown under 9-h short day extended with red+white+far-red (R+W+FR) LED lamps to achieve 10-, 11-, 13-, 15-, and 16-h photoperiods or a 4-h night interruption (NI).

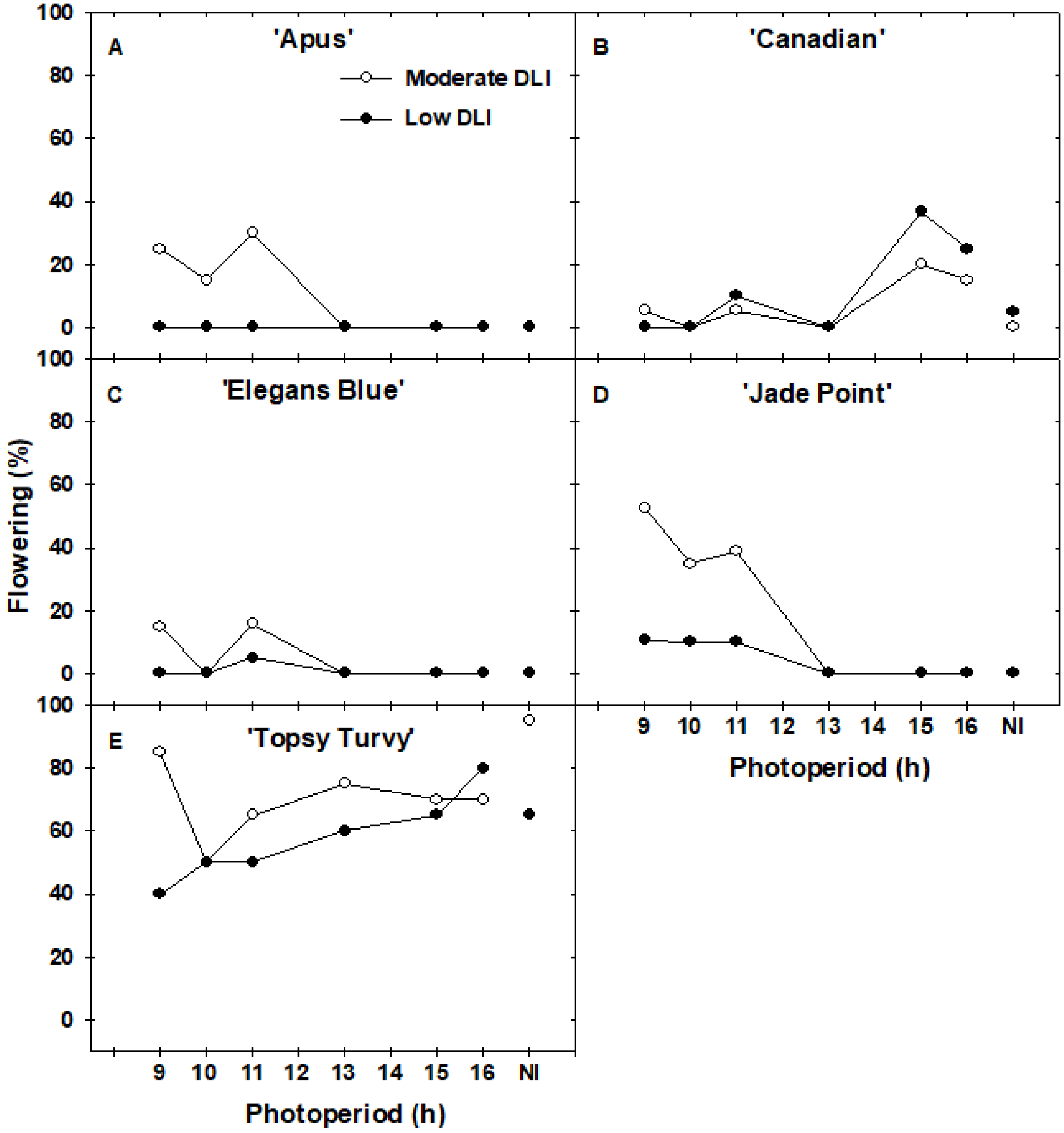
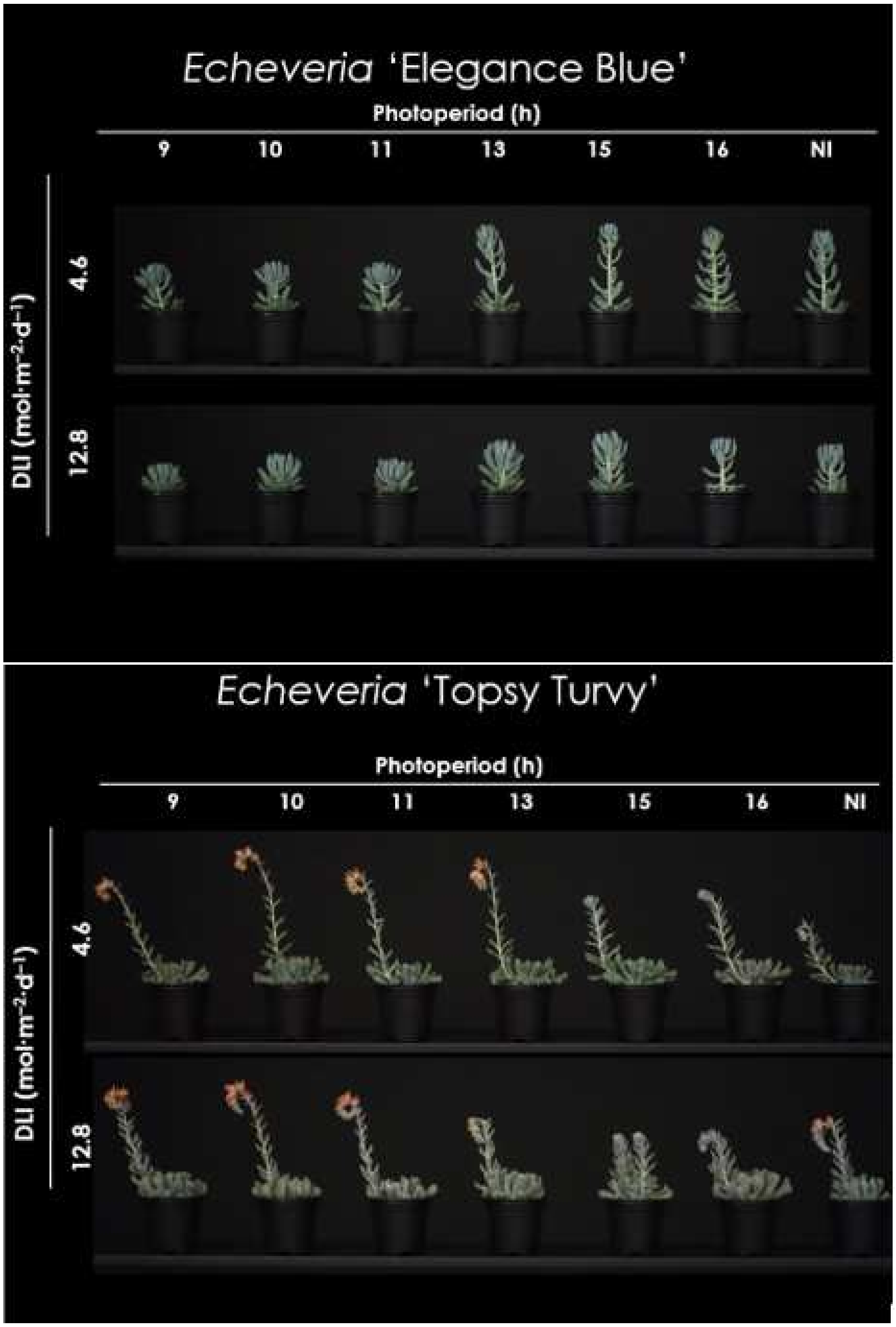


Figure I-6. Effect of moderate or low daily light integral, and photoperiod on *Echeveria* 'Topsy Turvy' and' Elegans Blue'.



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SECTION III

A single substrate drench of paclobutrazol can prevent undesired extension growth of potted succulents under low indoor radiation intensities

Anthony J. Soster and Roberto G. Lopez*

Department of Horticulture, 1066 Bogue Street, Michigan State University, East Lansing, MI 48824-1325, USA

*Corresponding author. Tel.: +1 517-353-0342. E-mail address: rglopez@msu.edu (R.G. Lopez).

Abstract

Low radiation intensities in indoor residential and office environments can lead to a loss of foliage color and leaves and excessive stem elongation of potted succulents. However, little research exists on how to prevent excessive stem elongation and increase post-production consumer success with succulents. Therefore, the objectives of our study were to 1) determine if one substrate plant growth regulator (PGR) drench of paclobutrazol could suppress excessive stem elongation and anthocyanin degradation of plants grown under radiation intensities common in indoor environments; 2) quantify the duration of stem elongation suppression for each rate of paclobutrazol applied; and 3) determine if radiation intensity impacts the efficacy of PGR drenches. Cuttings of round-leafed navel-wort ‘Silver Peak’ (*Cotyledon orbiculata*), Mexican hens and chicks ‘Elegance Blue’ (*Echeveria species*), tree houseleek ‘Stripe’ (*Aeonium leucoblepharum*), Graptoveria ‘Debbie’ (*Graptopetalum ×Echeveria*), and jade plant ‘Horntree Tricolor’ (*Crassula ovata*) were grown in a greenhouse with a 20 °C set point. When plants were marketable, 0, 2, 4, 6, or 8 mg·L^{-1} of paclobutrazol was applied as a substrate drench. Plants were then moved to one of two radiation intensity treatments created using no shade cloth or shade cloth that reduced the radiation intensity by 90%. Generally, height increased over time and more rapidly under the low daily light integral (DLI) of 1.8 $\text{mol·m}^{-2}\text{·d}^{-1}$ compared to the high DLI of 18.6 $\text{mol·m}^{-2}\text{·d}^{-1}$. However, the paclobutrazol substrate drench resulted in more compact *Cotyledon*, *Crassula*, *Echeveria*, and *Graptopetalum*. For example, untreated *Echeveria* were 19.1 cm taller than plants treated with 8 mg·L^{-1} paclobutrazol when grown under 1.8 $\text{mol·m}^{-2}\text{·d}^{-1}$. After 17 weeks, untreated *Cotyledon* grown under a low DLI were 33.4 cm taller than those treated with a PGR drench. However, *Aeonium* were approximately the same size throughout the course of the experiment regardless of the paclobutrazol drench rate. Flowering of *Aeonium*, *Cotyledon*, *Crassula*, and *Echeveria* was not influenced by any PGR or DLI treatment. However, *Graptopetalum* had 1.3

to 2.1 more flowers under a DLI of 18.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared to a DLI of 1.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Similarly, the branch number of untreated *Cotyledon*, *Crassula*, *Echeveria*, and *Graptopetalum* increased by 82, 128, 577, and 172%, respectively, under a DLI of 18.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared to a DLI of 1.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. The DLI had the greatest impact on succulent foliage color; however, a substrate drench of paclobutrazol helped retain color under a low DLI for *Cotyledon*. Our results suggest that a single paclobutrazol substrate drench of 2 and 8 $\text{mg}\cdot\text{L}^{-1}$ on *Echeveria* and *Graptopetalum*, and *Cotyledon* is suitable to reduce stem elongation associated under low radiation intensities. Additionally, paclobutrazol drenches marginally prevented anthocyanin degradation in some genera.

Keywords: *Cotyledon*, *Crassula*, daily light integral, *Echeveria*, plant growth regulator

Abbreviations: DLI, daily light integral; GA, gibberellic acid; MDT, mean daily temperature; PGR, plant growth regulator; *PPFD*, photosynthetic photon flux density.

Introduction

In recent years, there has been a resurgence in the demand for houseplants such as potted succulents. The Independent Garden Center 2020 State of the Industry Report indicated that 75% of respondents operated an indoor houseplant division (i.e., tropical foliage plants, succulents, and cacti) and reported a 7% increase in sales over 2019 (Spirgen, 2020). Consumers indicate the diversity of forms, colors, and textures, as well as drought tolerance, reduced pest pressure, and ease of maintenance are some of the reasons for their interest in succulents (WOS, 2016). However, plants grown in indoor environments typically require higher radiation intensities than are provided by consumers (Whiting et al., 2016). Radiation intensities in homes and offices can be reduced by up to 99% compared to outdoor or greenhouse environments (Giorgioni and Neretti, 2009). This reduction can be detrimental to succulent growth, color, and quality as low radiation intensities can lead to reduced plant dry mass (an indicator of net photosynthesis), increased internode length, and stunted development of storage organs (Corre, 1983).

Under low radiation intensities, optical density of chlorophyll concentration (Dong et al., 2014), average leaf area (Munir et al., 2004), and internode elongation increases compared to plants grown under high radiation intensities (Hersch et al., 2014). Erwin (1998) stated stem elongation is proportional to the logarithm of the irradiance that a plant is exposed to. Similarly, Munir et al. (2004) suggested the number of branches, flower buds, leaf area, and time to flower all show progressive decreases in quality as shade levels increase. Additionally, concentrations of other plant pigments, such as anthocyanins, can decrease due to reduced radiation intensity (Zhu, 2017).

Anthocyanins are plant pigments often used by pollinators and herbivores to identify plants, and by humans for aesthetic purposes (Stintzing and Carle, 2004). However, in some cases they serve as a screen, preventing damaging effects of high radiation levels without decreasing photosynthetic capacity (Pietrini et al., 2002). Cabahug et al. (2017) reported the percentage of red pixels in image analysis of Mexican hens and chicks (*Echeveria agavoides* and *E. marcus*) was 70% and 96%, respectively, when plants were grown under a photosynthetic daily light integral (DLI) of 7.5 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$, and <1% and 0%, respectively, under a DLI of 1.7 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$. This suggests that low radiation intensities of 35 $\mathrm{\mu mol \cdot m^{-2} \cdot s^{-1}}$, commonly found in indoor environments, can reduce anthocyanin concentration in *Echeveria* leaf tissues (Cabahug et al., 2017). A separate study by Cruz et al. (2012) found that the relative anthocyanin concentrations in leaf of luck (*Kalanchoe brasiliensis*) and leaf of good fortune (*K. pinnata*) petioles were 1.0 mg/100 g and 1.6 mg/100 g in 25% and 70% full sunlight, respectively. However, the authors found no difference in anthocyanin content measured in the leaf blades of either species of *Kalanchoe* (Cruz et al., 2012). This conclusion provides evidence that certain tissues may have a greater affinity for producing or storing anthocyanins regardless of radiation intensity, and that radiation intensity has a marked effect on anthocyanin accumulation in some species of *Kalanchoe*. Changes in leaf color are often quantified in horticulture though the use of colorimeters to measure the reflectance properties of leaves (Owen and Lopez, 2015). This can be done by measuring the CIE L*, a*, and b* values to measure the leaf lightness, and the red to green and blue to yellow ratios. L* measures white to black where black is 0 and white is 100, a* measure the green to red ratio, where green is –60 and red is +60, and b* measures the blue to yellow ratio, where blue is –60 and yellow is +60, respectively.

Hormones exist naturally in many plant tissues, carrying out various cellular functions including stem elongation, root proliferation, and apical dominance (Leopold and Nooden, 1984). Plant growth regulators (PGRs) are chemical compounds that regulate growth and developmental processes by promoting or suppressing extension growth, germination, branching, or flowering when applied to crops (Camberato et al., 2011). Gibberellins (GA) are a group of plant hormones that are involved in cell elongation and division which results in subsequent stem elongation (Sauter and Kende, 1992). One important class of PGRs are those that inhibit gibberellin biosynthesis in plant tissues. These PGRs include the chemicals pyrimidines, 4-pyridines, and triazoles (Grossmann, 1992). Application methods can vary depending on the type of chemical and desired effect. Drenches and sprays are the two most common PGR methods of applications; a spray is an application to the leaves and/ or stems, while a drench applies the PGR to the growing substrate where it can be absorbed by the roots. Typically, lower chemical concentrations are needed for drenches to attain the same effect as a spray, and the efficacy of drench applications can persist longer than sprays (Whipker, 2021). For example, drench applications of paclobutrazol to pink lady (*Dissotis rotundifolia*) and glory bush (*Tibouchina fothergillae*) resulted in a smaller finished plant volume at rates of 0, 0.125, 0.25, or 0.5 mg of active ingredient compared to equal application rates applied as a spray (Hawkins et al., 2015). The application rate or volume can be modified to accentuate the desired plant morphology or architecture.

Few PGR recommendations exist for succulents, other than a general recommendation that growers spray 20 $\text{mg}\cdot\text{L}^{-1}$ of 0.4% paclobutrazol prior to shipping to prevent deterioration as the product moves through the supply chain (Dümmen Orange, 2018). Hwang et al. (2008) determined that soaking cuttings of *Kalanchoe* ‘Ranko’ and ‘Gold Strike’ in a 0.5 $\text{mg}\cdot\text{L}^{-1}$ solution of paclobutrazol resulted in 9% and 13% shorter internode lengths compared to plants treated with 0 $\text{mg}\cdot\text{L}^{-1}$, respectively, when observed 15 weeks after treatment. Similarly, Currey and Erwin (2012) reported that a 40 $\text{mg}\cdot\text{L}^{-1}$ spray application of paclobutrazol on *Kalanchoe rosei*, *K. streptantha*, *K. fedtschenkoi*, *K. pumila*, *K. manginii*, *and K. rotundifolia* resulted in a 17, 24, 31, 39, 53 and 62% reduction in stem elongation, respectively, compared to plants sprayed with water (control). Additionally, regardless of concentration, spray applications of paclobutrazol did not influence branch number across the species investigated (Currey and Erwin, 2012).

Light acclimation is frequently used in tropical plant production in order to lower the light compensation point and improve plant quality under subsequent low radiation conditions found in indoor environments. Turner et al. (1987) determined that post-production acclimation of weeping fig (*Ficus benjamina*) resulted in a reduction of percent cumulative leaf drop as shade intensity increased from 0% to 80%. Furthermore, reducing radiation intensity during the production phase results in little to no change in post-production physiology. For example, reducing the maximum photosynthetic photon flux density (*PPFD*) from 550 to 285 $\mu mol \cdot m^{-2} \cdot s^{-1}$ during the production of money tree (*Pachira aquatica*) had no impact on height or mean internode length after 6 months under simulated indoor radiation conditions of 0.77 $mol \cdot m^{-2} \cdot d^{-1}$ (Li et al., 2009). Interestingly, money tree treated with a single spray application of 50 $mg \cdot L^{-1}$ of paclobutrazol at the end of production resulted in plants that were 21 to 26 cm shorter than untreated plants after 6 months under a DLI of 0.77 $mol \cdot m^{-2} \cdot d^{-1}$ (Li et al., 2009).

To our knowledge, no work has been conducted to investigate if a single, high-concentration, pre-shipping paclobutrazol drench on potted succulents can prevent excessive extension growth when plants are grown under low radiation intensities similar to those in homes and offices. Our objectives were to 1) establish if a single paclobutrazol drench can prevent excessive growth and anthocyanin degradation of several succulent genera when subsequently grown under low and high radiation intensities; 2) determine the duration of stem elongation suppression for each paclobutrazol drench rate; and 3) quantify if subsequent radiation intensity influences the efficacy of paclobutrazol drenches.

Materials and methods

Cuttings of round-leafed navel-wort 'Silver Peak' (*Cotyledon orbiculata*), Mexican hens and chicks 'Elegance Blue' (*Echeveria species*), tree houseleek 'Stripe' (*Aeonium leucoblepharum*), Graptoveria 'Debbie' (*Graptopetalum* ×*Echeveria*), and jade plant 'Horntree Tricolor' (*Crassula ovata*) were received from a commercial propagator (Dümmen Orange, Columbus, OH) on 21 Jan. 2020, 28 Jan. 2020, 11 Feb. 2020, and 03 Mar. 2020. Cuttings were inserted into 18-01 cell packs (373-ml) (East Jordan Plastics Inc., East Jordan, MI) the day after they were received. The containers were filled with a combination of 75% commercial soilless substrate [70% peat moss, 21% perlite, and 9% vermiculite substrate (Suremix; Michigan Grower Products Inc., Galesburg, MI)] and 25% coarse perlite (Coarse Perlite; Perlite Vermiculite Packaging Industries Inc., North Bloomfield, OH). After transplant, a foliar spray of indole-3-butyric acid (Advocate; Fine Americas, Inc., Walnut Creek, CA) and a surfactant (Capsil; Aquatrols, Paulsboro, NJ) at a concentration of 75 $mg \cdot L^{-1}$ at a volume of 0.2 $L \cdot m^{-2}$ was applied to the cuttings to promote uniform rooting. Trays were placed in a glass-glazed greenhouse at Michigan State University (East Lansing, MI; lat. 43 °N). An environmental control system (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada) controlled exhaust fans, evaporative cooling pads, radiant hot-water heating and supplemental lighting. High-pressure sodium lamps (LR48877; P.L. Light Systems, Beamsville, ON, Canada) maintained a 16-h photoperiod and provided a *PPFD* of 60.6 ± 5.2 $\mu mol \cdot m^{-2} \cdot s^{-1}$ when the outdoor radiation intensity was below ≈440 $\mu mol \cdot m^{-2} \cdot s^{-1}$. The mean daily temperature (MDT) and DLI were 21.6 ± 1.3 °C and 16.8 ± 6.1 $mol \cdot m^{-2} \cdot s^{-1}$, respectively, for replications 1 and 2. Plants were irrigated as necessary with reverse osmosis water blended with MSU Orchid RO Special fertilizer (13 N–1.3 P–12.5 K; Greencare Fertilizers, Inc., Kankakee, IL) containing ($mg \cdot L^{-1}$): 125 N, 13 P, 121 K, 78 Ca, 19 Mg, 0.17 B and Mo, 0.43 Cu and Zn, 1.7 Fe, and 0.85 Mn.

Rooted cuttings of *Cotyledon*, *Crassula*, *Echeveria*, *Aeonium*, and *Graptopetalum* were transplanted after 7, 7, 7, 10, and 10 weeks, respectively, into 11-cm round (600-mL) containers filled with the substrate described in Section 2.1. When each genus was marketable, a substrate drench of 74 mL was applied to each container at a concentration of 0, 2, 4, 6, or 8 mg·L^{-1} paclobutrazol (Piccolo; Fine Americas, Inc., Walnut Creek, CA) in order to provide 0.075, 0.15, 0.3, 0.45, or 0.6 mg of active ingredient per container, respectively. Two days later, plants were transferred to one of two radiation intensity treatments created using either two layers of shade cloth (Solaro 8635 O FB and Solaro 2620 O E AW; Ludvig Svensson, Kinna, Sweden), which reduced the radiation intensity by ≈90%, or no shade cloth. A shielded and aspirated 0.13-mm type E thermocouple (Omega Engineering, Stamford, CT) and a quantum sensor (LI-190R; LI-COR, Lincoln, NE) measured the MDT and *PPFD*, respectively. Every 15-s, a data-logger (CR-1000; Campbell Scientific, Logan, UT) collected data from these sensors and hourly means were recorded. MDT and DLI ± SD are provided in Table 1.

After 7 (*Aeonium*, *Cotyledon*, *Crassula*, *Echeveria*, *Graptopetalum*), 13 (*Aeonium*, *Cotyledon*, *Crassula*, *Echeveria*, *Graptopetalum*), and 15 (*Graptopetalum*) or 17 (*Cotyledon*, *Echeveria*) weeks, leaf and branch number, height from the base of the container to the tallest point on the plant, reproductive data, plant diameter at the widest point and perpendicular from the widest point were recorded. These data were measured repeatedly throughout the course of the experiment. At the end of the experiment growth index was calculated (GI = {plant height + [(diameter 1 + diameter 2)/2]}/2) according to Krug et al. (2010). Leaf color of the youngest leaves of *Graptopetalum*, *Aeonium*, and *Cotyledon* were measured using a handheld colorimeter (BC-10; Konica Minolta Sensing, Inc., Ramsey, NJ) which provided the CIELAB L*a*b* color coordinates. Adjusted hue angle (h°) was calculated according to McLellan et al. (1994).

The experiment was organized in a randomized complete-block design with a two-way factorial arrangement with repeated measures. Plants were blocked by PGR rate (five levels) and DLI (two levels), with 10 randomly selected plants per treatment combination. The experiment was performed twice simultaneously for the five genera evaluated. Data were analyzed with SAS version 9.4 (SAS Institute, Inc., Cary, NC). Mixed model procedure (PROC MIXED) was used for the color, branch and flower number data, and pairwise comparisons were performed with Tukey-Kramer difference test ($P \leq 0.05$). The regression procedure (PROC REG) was used to analyze linear and quadratic regression models. Data were analyzed separately by genera and interaction among genera was not evaluated. Regression model equations are provided in Table 2.

Results

Under a low DLI of 1.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, height of *Cotyledon* increased linearly over time regardless of paclobutrazol substrate drench rate compared to plants treated with the same rates under a DLI of 18 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 2; Fig. 1). However, *Cotyledon* plants treated with 6 and 8 $\text{mg}\cdot\text{L}^{-1}$ of paclobutrazol under the low DLI were much more compact (≤30 cm) than untreated plants under the high DLI. After 17 weeks under a high DLI, there was little to no extension growth when *Cotyledon* was treated with 6 and 8 $\text{mg}\cdot\text{L}^{-1}$ of paclobutrazol (Fig. 1B). Height of *Echeveria* treated with paclobutrazol drench rates ≥2 $\text{mg}\cdot\text{L}^{-1}$ slightly increased linearly or remained the same (≤ 15 cm) under a low or high DLI (Table 2; Fig. 2A and C). Height of untreated *Echeveria* under a DLI of 1.8 and 18 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ after 17 weeks was 33.2 cm and 20.6 cm, respectively (Figs. 2A and C). In contrast, the height of *Crassula* was greater at the end of the experiment under a high DLI compared to a low DLI regardless of the PGR rate (Fig. 2B and D). Height of untreated *Crassula* was 22.0 and 19.7 cm under low and high DLIs, respectively (Fig. 2B and D). Similarly, there were few changes in the growth index of *Aeonium* over the course of the experiment (Fig. 3A and C). The growth index of *Echeveria* followed a similar trend to height (Fig. 3B and D).

Aeonium, *Cotyledon*, and *Crassula* did not develop any inflorescences or flowers during the course of the experiment. Only one *Echeveria* plant flowered. *Graptopetalum* produced 253% more inflorescences under a DLI of 18.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared to a DLI of 1.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 4). Branch number of *Crassula*, *Cotyledon*, *Echeveria*, and *Graptopetalum* was greatest under a DLI of 18.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Table 4). For *Cotyledon*, plants developed 2.9 more branches per plant as the PGR drench rate increased from 0 to 8 $\text{mg}\cdot\text{L}^{-1}$ under the higher DLI (Table 4). In contrast, untreated *Graptopetalum* under the high DLI had more branches compared to plants treated with a paclobutrazol drench.

CIELAB color values varied greatly across DLIs and some differences were observed across PGR drench rates (Table 4). For untreated *Aeonium*, h° was 412.4° when grown under a high DLI compared to 113.5° for plants grown under a low DLI (Table 4). Under a high DLI, the h° of untreated *Aeonium* was only 9.6° greater than plants treated with an 8 $\text{mg}\cdot\text{L}^{-1}$ drench (Table 4). PGR drench rate did not influence the h° of *Graptopetalum*, regardless of DLI (Table 4). However, h° was ≈356.8° on average for plants grown under a high DLI, compared to 139.8° for those grown under a low DLI (Table 4). The L* value of *Aeonium* were similar across all treatments (Table 4). The a* and b* values of *Aeonium Cotyledon*, and *Graptopetalum* leaves were impacted by DLI (Table 4). However, few differences were observed between PGR application rates. For example, the b* of *Cotyledon* treated with a 0 $\text{mg}\cdot\text{L}^{-1}$ drench was 8.7 greater when grown under a high DLI compared to a low DLI (Table 4).

Discussion

High-quality floriculture crops are compact and well branched, have deep green, colorful or variegated foliage; they fill in the container; are free of pests and diseases; and either have an abundance or absence of flowers, depending upon the market (Runkle, 2011). Therefore, plants with excessive internode elongation or chlorotic, pale, or dull foliage color are considered to be of poor quality. Radiation intensities found in indoor households and offices can be 1% of those recorded outdoors or in greenhouses (Giorgioni and Neretti, 2009). Some researchers have quantified indoor radiation intensities ranging from 0.16 $mol \cdot m^{-2} \cdot d^{-1}$ to as high as 7.8 $mol \cdot m^{-2} \cdot d^{-1}$ (Kim et al., 2012; Kubatsch et al., 2007). These low photosynthetically active radiation intensities in the consumer environment can have a profound impact on the overall health, lifespan, and quality of house plants including their morphology, foliage color, and leaf size. Most notably, there is a dramatic increase in internode length (Erwin, 1998; Corre, 1983) and a decrease in branch and flower number (Munir et al., 2004) under low radiation intensities. Light acclimation is a method of increasing the post-production quality and life of common house plants (Chen et al., 2005). For some plants, reducing radiation intensity in the final few weeks of production prior to shipping can result in a decrease in total leaf senescence (Sawwan and Ghunem, 1999; Turner et al., 1986).

Anthocyanins are natural plant pigments that can function to prevent damage from high radiation levels (Pietrini et al., 2002). While anthocyanins are well known for their impacts on flower color, the impacts on foliage color are not as well researched. Close and Beadle (2003) reported anthocyanins accumulate in young foliage, in response to nutrient deficiencies or as a defense against herbivory. Additionally, temperature, blue and ultra-violet radiation, and radiation intensity play a role in the promotion or suppression of anthocyanin production (Gu et al., 2019). For instance, anthocyanin production in red leaf lettuce (*Lactuca sativa* ‘Red Salad Bowl’) is reduced when grow under radiation intensities below 3.7 mol·m^{-2}·d^{-1} (Paz et al., 2019). Furthermore, low radiation intensities have been attributed to a reduction in anthocyanin concentration in some succulents (Cabahug et al., 2017).

One common method of measuring color of fruits and vegetables in postharvest physiology is the reporting of the CIELAB values measured by a colorimeter (Paz et al., 2019; Owen and Lopez, 2015; Mansuroglu et al., 2009; McGuire 1992). However, reporting L*, a*, and b* do not provide an intuitive measure of color, therefore h° is a better indicator. The calculation of h° involves several steps in order to convert numeric measurements into a single unit in the three-dimensional color space (McGuire, 1992). First theta must be calculated by taking the arctangent of the b* and a* color values, then measurements are converted into degrees and adjusted based on the sign of a* and b* (McGuire, 1992). However, due to the limitations of arctangents, comparisons of negative and positive values are illogical, and a correction factor is needed for meaningful transformation (McLellan et al., 1994). Adjusting the scale such that h° can be greater than 360° allows for meaningful statistical interpretation (McLellan et al., 1994).

Our data were similar to those reported by Cabahug et al. (2017), as L* was reduced under low radiation intensities. Anthocyanin concentrations decreased from 0.93 to 0.28 mg/100g for *Echeveria agavoides* as radiation intensities were reduced from 150 to 35 µmol·m^{-2}·s^{-1} (Cabahug et al., 2017). Similarly, Cruz et al. (2012) reported anthocyanin concentration in leaf petioles of *Kalanchoe brasiliensis* and *K. pinnata* was reduced as shade was increased from 25% to 70%. However, they found no differences in leaf blade anthocyanin concentration, suggesting that different plant organs have greater fluctuations in secondary metabolites in response to DLI. While we observed some differences in color values under various PGR concentrations, they were not as pronounced as the differences under high and low DLIs. Mansuroglu et al. (2009) reported similar results as paclobutrazol sprays influenced leaf color of oriental knight's spur (*Consolida orientalis*) at concentrations of 125, 250, and 500 $mg{\cdot}L^{-1}$. Regardless of PGR rate, L* was 4.1 to 4.7 CIELAB units lower than the untreated control (Mansuroglu et al., 2009). Flower color was similarly impacted, but only at rates above 500 $mg{\cdot}L^{-1}$, where L* was 5.29 CIELAB units lower than the untreated control (Mansuroglu et al., 2009).

Changes in the foliage color of *Cotyledon* in response to DLI were due to the change of the cuticle from a waxy silver-gray, which gives the cultivar its name 'Silver Peak', to a pale green. Similarly, Robinson et al. (1993) and Barker et al. (1997) reported epidermal wax of *Cotyledon* was a photoprotectant that reduced total leaf reflectance under high radiation intensities. For example, *Cotyledon orbiculata* grown under 1,300 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ had 42% higher leaf reflectance than those grown under 350 $\mu mol{\cdot}m^{-2}{\cdot}s^{-1}$ (Robinson et al., 1993). While our colorimeter measurements were able to identify differences between *Cotyledon* grown under different DLIs, the differences were not as pronounced as those observed in *Aeonium* and *Graptopetalum*. Quantification of external waxes may be a useful metric in identifying acclimation to the radiation environment for some succulent genera.

Synthetically derived PGRs are commonly used to manipulate plant morphology to meet market specifications. Plant growth retardants, a subclass of PGRs, function to disrupt GA biosynthesis, resulting in increased branching, decreased internode length, and smaller leaves (Camberato et al., 2011). Research on common bedding plant crops shows the effectiveness of PGRs on plant growth and development (Hawkins et al., 2015). In the U.S., typical paclobutrazol drench recommendations for general bedding plants such as New Guinea impatiens (*Impatiens hawkeri*) range from 0.25 to 2.0 mg·L^{-1}, while recommendations for more aggressive plants, such as sweet potato vine (*Ipomoea batatas*), are as high as 8 mg·L^{-1} (Whipker, 2021). Some work has been conducted investigating the effects of PGRs on succulents during production. Currey and Erwin (2012) reported spray applications of paclobutrazol at rates of 10, 20 or 40 mg·L^{-1} on several species of *Kalanchoe* reduced stem elongation. Our results were in agreement with Hwang et al. (2008) and Currey and Erwin (2012), as we observed a substantial decrease in stem elongation for *Echeveria*, *Graptoveria*, and *Cotyledon*. However, PGR application was not necessarily beneficial for all crops studied. For example, the application of PGRs to *Echeveria* resulted in lower leaf yellowing and senescence, reducing quality (Fig. 4). Additionally, for *Aeonium* and *Crassula*, a PGR drench was not necessary as the plants did not elongate under a low radiation environment. While our results provide evidence that a ≥4 mg·L^{-1} substrate drench of paclobutrazol can aide in preventing stem elongation, it cannot prevent anthocyanin degradation or the reduction in branch or flower number. Similarly, Currey and Erwin (2012) indicated spray applications did not influence branch number in several *Kalanchoe* species. Few practical recommendations exist for other genera of succulents. Therefore, more research is needed on other methods to improve post-production quality of greenhouse grown succulents.

Delivering greater value to consumers by promoting foliage plant attributes, such as air filtration capabilities, sustainable production methods, and local production, has been shown to increase the likeliness to purchase (Rihn et al., 2015). Increasing the post-production quality of indoor foliage plants can also deliver greater value to consumers by extending the life and aesthetic value of the plant in the home or office environment. A consumer who is satisfied with their purchase is more likely to become a repeat customer, suggesting that increasing consumer satisfaction could lead to more and larger purchases (Hicks, 2005).

Our study provides evidence a single ≥4 $mg \cdot L^{-1}$ substrate drench of paclobutrazol, which is generally higher than the recommended rate for most bedding plants, can be used on some succulent genera to reduce excessive stem elongation associated with low indoor radiation intensities. We also determined a low radiation intensity did not lead to excessive stem elongation of *Crassula* and *Aeonium* and, therefore, a paclobutrazol drench is not necessary. However, other genera and species of succulents may respond more or less favorably to chemical growth regulation. Additional research investigating the effects of other PGRs such as ancymidol, chlormequat chloride, ethephon, flurprimidol, and uniconazole on succulent growth and development is also needed. Additionally, PGRs that reduce the degradation of anthocyanins such as prohydrojasmon should be investigated on potted succulent to determine if they can inhibit their post-production reduction in quality.

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Americas, Inc. The use of trade names in this publication does not imply endorsement by Michigan State University of products named nor criticism of similar ones not mentioned.

APPENDIX

Table II-1. Mean (± SD) for the daily light integral (DLI) and mean daily temperature (MDT) of succulents grown under natural solar radiation or two layers of shade cloth.

DLI treatment	Rep	DLI ($mol \cdot m^{-2} \cdot d^{-1}$)	Greenhouse air MDT (ºC)
Low	1	1.8 ± 0.5	23.2 ± 2.5
	2	1.8 ± 0.5	23.1 ± 2.2
High	1	18.9 ± 5.5	25.1 ± 3.0
	2	18.2 ± 4.9	23.2 ± 2.4

Table II-2. Repeated measures regression equations for *Aeonium*, *Cotyledon*, *Crassula*, *Echeveria* and *Graptopetalum* that received a substrate plant growth regulator (PGR) drench of paclobutrazol at 0, 2, 4, 6, or 8 mg·L^{-1} and grown under a low and high daily light integral (DLI).

Genus	Parameter	DLI	PGR rate (mg·L^{-1})	Regression equation
Aeonium				
	Growth index			
		High	0	$y = 13.75 + 1.92x - 0.62x^2$
			2	$y = 13.36 + 0.52x$
			4	$y = 13.67 + 0.49x$
			6	$y = 13.26 + 1.23x - 0.45x^2$
			8	$y = 13.74 + 1.57x - 0.67x^2$
		Low	0	$y = 10.32 + 2.01x - 0.75x^2$
			2	NS
			4	NS
			6	$y = 13.61 + 0.73x - 0.54x^2$
			8	NS
Echeveria				
	Average height			
		High	0	$y = 14.47 + 2.07x$
			2	$y = 14.35 + 0.20x$
			4	NS
			6	NS
			8	$y = 14.79 - 0.15x$
		Low	0	$y = 16.91 + 6.53x$
			2	NS
			4	$y = 14.71 - 0.27x$
			6	$y = 14.83 - 0.29x$
			8	$y = 15.05 - 0.31x$

Table II-2 (cont'd)

	Growth index			
		High	0	$y = 11.57 + 1.85x$
			2	$y = 11.41 + 0.39x$
			4	$y = 11.23 + 1.10x - 0.28x^2$
			6	$y = 11.16 + 1.30x - 0.37x^2$
			8	$y = 11.43 + 1.09x - 0.32x^2$
		Low	0	$y = 12.37 + 4.25x$
			2	$y = 11.07 + 1.85x - 0.46x^2$
			4	$y = 11.29 + 1.18x - 0.35x^2$
			6	$y = 11.48 + 1.34x - 0.39x^2$
			8	$y = 11.67 + 1.10x - 0.35x^2$
Cotyledon				
	Average height			
		High	0	$y = 23.94 + 3.58x$
			2	$y = 22.85 + 1.76x$
			4	$y = 23.01 + 0.83x$
			6	NS
			8	$y = 23.96 - 0.40x$
		Low	0	$y = 24.58 + 11.59x$
			2	$y = 23.01 + 6.62x$
			4	$y = 23.59 + 3.88x$
			6	$y = 23.39 + 2.52x$
			8	$y = 23.18 + 1.73x$
Crassula				
	Average height			

Table II-2 (cont'd)

High	0	y = 17.83 + 2.21x
	2	y = 17.66 + 0.70x
	4	y = 17.38 + 0.78x
	6	y = 17.88 + 0.69x
	8	y = 17.84 + 0.76x
Low	0	y = 17.76 + 1.01x
	2	y = 17.55 + 0.34x
	4	NS
	6	NS
	8	NS

Table II-3. Analysis of variance for CIE L*a*b* color coordinates, hue angle (h°), final branch, and final flower number of *Aeonium*, *Cotyledon*, *Crassula*, *Echeveria* and *Graptopetalum* receiving a growing substrate plant growth regulator (PGR) drench of paclobutrazol at 0, 2, 4, 6, or 8 mg·L^{-1} and grown under a low and high daily light integral (DLI).

	DLI	PGR	DLI × PGR
		Aeonium	
L	*^{z}	NS	NS
a	***	**	NS
b	***	NS	NS
h°	***	**	NS
		Cotyledon	
L	***	NS	NS
a	***	NS	*
b	***	NS	**
h°	NS	NS	NS
Branch number	***	NS	***
		Crassula	
Branch number	***	*	NS
		Echeveria	
Branch number	***	NS	NS
		Graptopetalum	
L	***	***	NS
a	***	*	**
b	***	NS	NS
h°	***	NS	NS
Branch number	***	***	NS
Flower number	***	NS	NS

Table II-3 (cont'd)

^{z}NS, *, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

Table II-4. Effect of high or low daily light integral (DLI) and a substrate drench of 0, 2, 4, 6, or 8 mg·L^{-1} paclobutrazol on CIE L*a*b* color coordinates, hue angle (h°) branch and flower number of *Aeonium*, *Cotyledon*, *Crassula*, *Echeveria* and *Graptopetalum*.

	Paclobutrazol rate (mg·L^{-1})				
DLI (mol·m^{-2}·d^{-1})	0	2	4	6	8
			Aeonium		
			h°		
1.8	113.5 c	108.7 c	111.6 c	109.8 c	109.7 c
18.6	412.4 a	404.3 ab	403.5 ab	397.5 ab	402.8 b
			L*		
1.8	42.7 a	42.5 a	42.3 a	42.3 a	42.4 a
18.6	43.0 a	41.3 a	41.0 a	41.9 a	41.7 a
			a*		
1.8	-4.5 c	-3.3 c	-3.7 c	-3.5 c	-3.0 c
18.6	6.9 b	7.8 ab	7.6 ab	9.9 a	8.5 ab
			b*		
1.8	9.5 a	9.4 a	9.3 ab	9.3 a	8.4 abc
18.6	8.9 abc	7.6 abc	7.2 c	7.3 bc	7.8 abc
			Cotyledon		
			h°		
1.8	120.5 e	121.7 e	123.0 de	125.2 de	124.3 de
18.6	143.6 a	139.9 ab	134.2 bc	130.1 cd	131.0 cd
			L*		
1.8	48.8 c	50.3 bc	50.7 bc	52.9 b	52.8 b
18.6	69.3 a	68.5 a	67.8 a	66.4 a	66.3 a
			a*		
1.8	-5.2 c	-4.2 b	-4.2 b	-3.8 b	-3.7 b

Table II-4 (cont’d)

18.6	-1.7 a	-1.8 a	-1.7 a	-1.8 a	-2.0 a
b*					
1.8	10.0 a	7.2 b	6.8 b	5.6 b	5.7 b
18.6	1.3 c	1.5 c	1.8 c	2.2 c	2.5 c
Branch (no.)					
1.8	9.9 d	9.0 d	9.0 d	8.4 d	8.7 d
18.6	14.9 c	15.6 bc	16.5 abc	17.2 ab	17.8 a
Crassula					
Branch (no.)					
1.8	3.0 b	2.5 b	2.3 b	2.7 b	2.3 b
18.6	6.2 a	6.1 a	5.1 a	6.3 a	5.6 a
Echeveria					
Branch (no.)					
1.8	0.7 c	0.7 c	0.7 c	0.6 c	0.4 c
18.6	5.3 a	3.7 b	3.8 ab	4.1 ab	4.1 ab
Graptopetalum					
h°					
1.8	136.9 b	142.9 b	144.2 b	139.7 b	135.3 b
18.6	356.6 a	346.6 a	373.2 a	361.8 a	345.9 a
L*					
1.8	45.5 b	44.4 b	44.4 b	43.8 b	43.4 b
18.6	48.4 a	44.9 b	45.6 b	45.0 b	45.2 b
a*					
1.8	-3.3 c	-3.5 c	-3.4 c	-3.6 c	-3.5 c
18.6	1.6 b	3.6 a	4.2 a	3.5 a	3.3 a
b*					

Table II-4 (cont'd)

1.8	3.7 a	2.8 ab	2.7 ab	3.3 a	3.6 a
18.6	0.0 c	-0.1 c	0.4 c	0.3 c	1.0 bc
Branch (no.)					
1.8	2.3 bc	0.5 d	1.1 cd	0.8 d	1.1 cd
18.6	4.6 a	2.6 b	2.6 b	2.8 b	3.2 b
Flower (no.)					
1.8	0.8 b	0.9 b	0.9 b	0.5 b	0.5 b
18.6	2.1 a	2.6 a	3.0 a	2.4 a	2.6 a

Figure II-1. Average height of *Cotyledon* treated with a substrate drench of 0, 2, 4, 6, and 8 mg·L^{-1} paclobutrazol and grown under a low (A) or high DLI (B). Data were pooled across replications. Open symbols indicate high DLI, filled symbols indicate low DLI. NS, *, **, *** indicate nonsignificant or significant at $P \leq 0.05$, 0.01, and 0.001, respectively. Error bars indicate standard error of the mean. R represents quadratic regression and r represents linear regression.

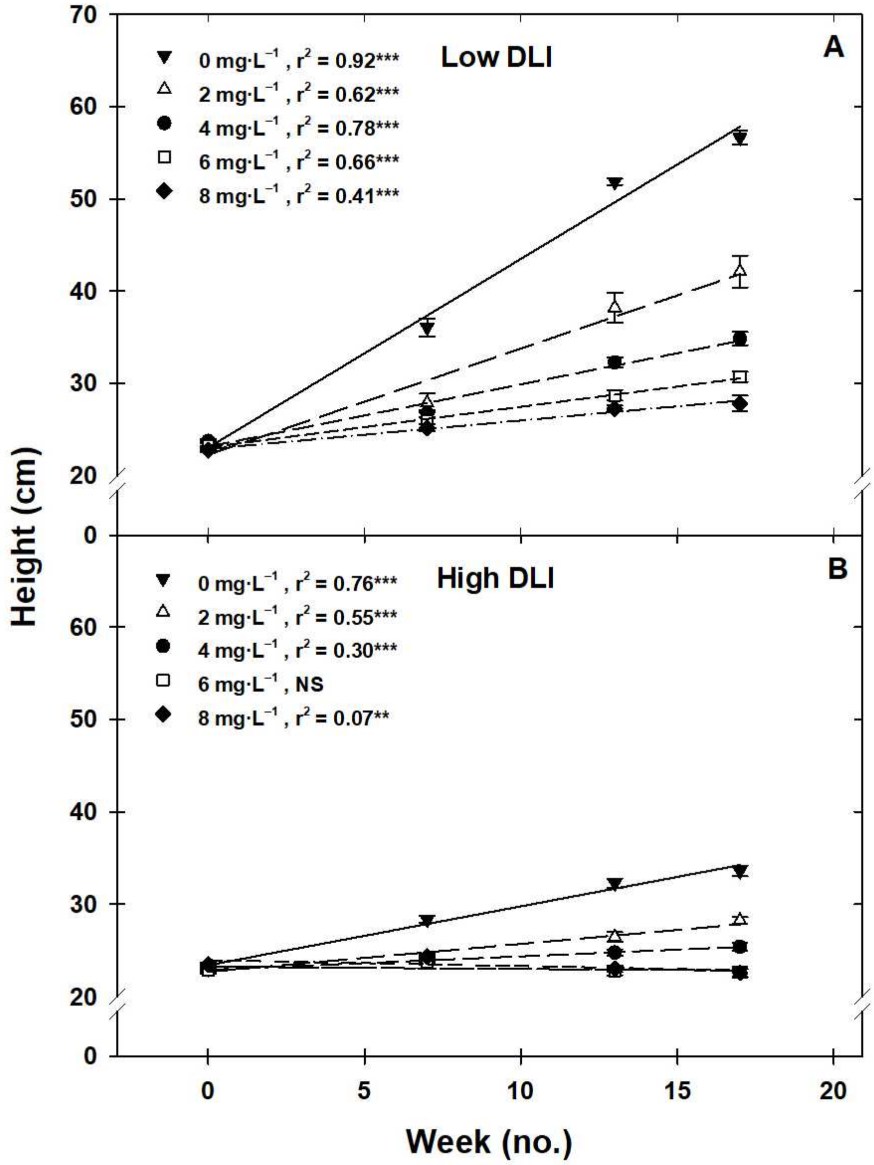


Figure II-2. Average height for *Crassula* (B and D) and *Echeveria* (A and C) treated with a substrate drench of 0, 2, 4, 6, and 8 mg·L^{-1} paclobutrazol and grown under a low (A and B) or high DLI (C and D). Data were pooled by replication. NS, *, **, *** indicate nonsignificant or significant at P ≤ 0.05, 0.01, and 0.001, respectively. Error bars indicate standard error. R represents quadratic regression and r represents linear regression.

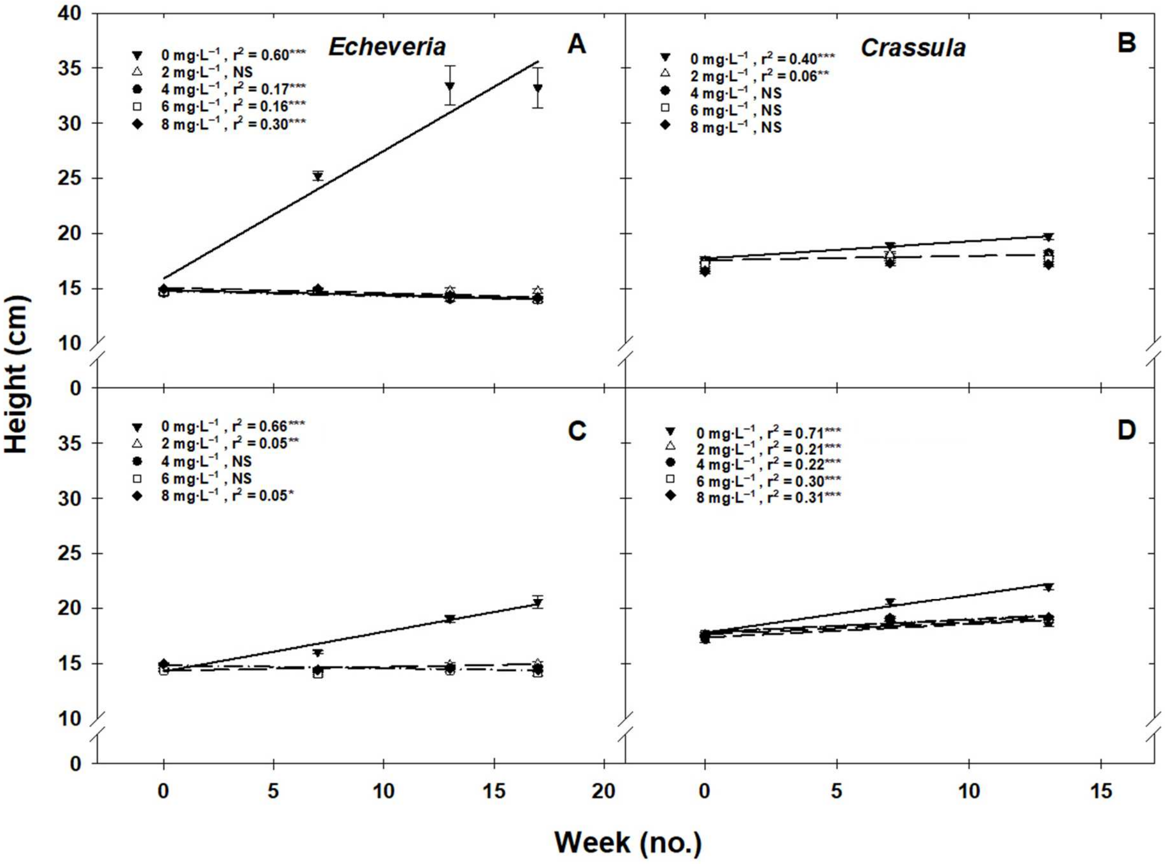


Figure II-3. Growth index of *Aeonium* (A and C) and *Echeveria* (B and D) treated with a substrate drench of 0, 2, 4, 6, and 8 mg·L^{-1} paclobutrazol and grown under a low (A and B) or high DLI (C and D). Data were pooled by replication. NS, *, **, *** indicate nonsignificant or significant at P ≤ 0.05, 0.01, and 0.001, respectively. Error bars indicate standard error. Lower case r represents linear regression, upper case r represents quadratic regression.

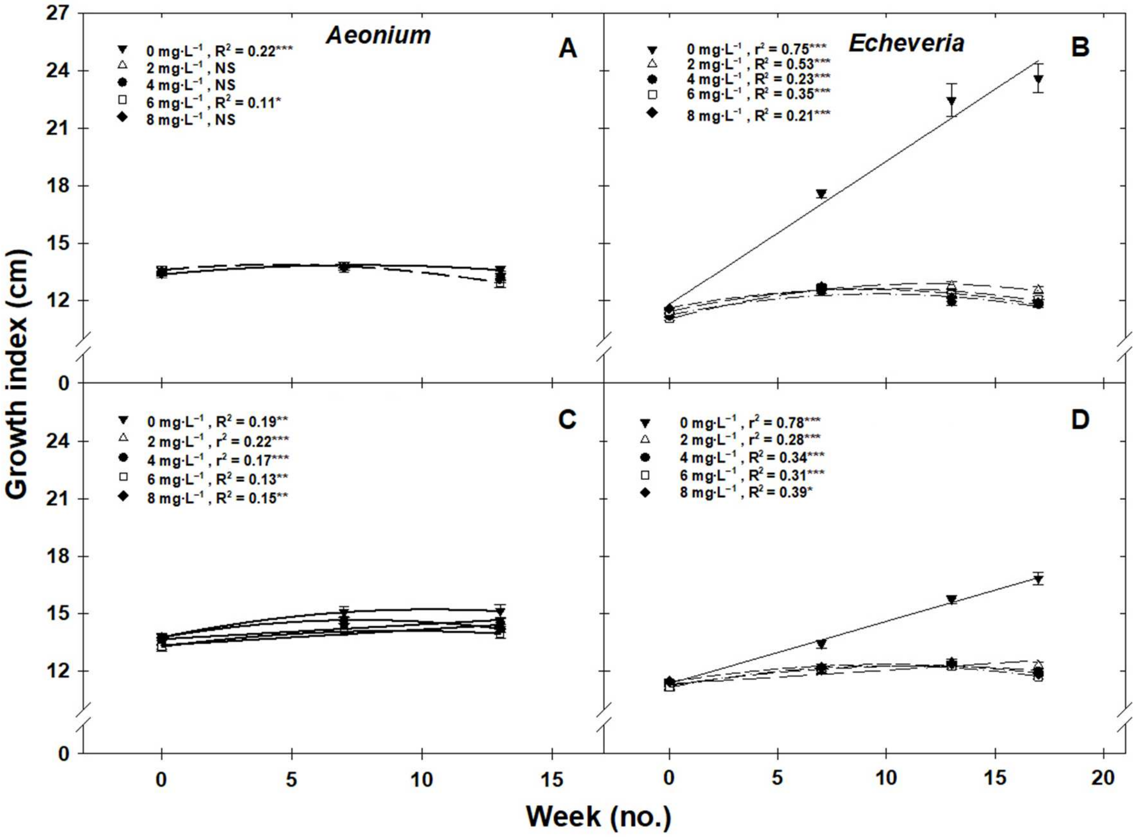
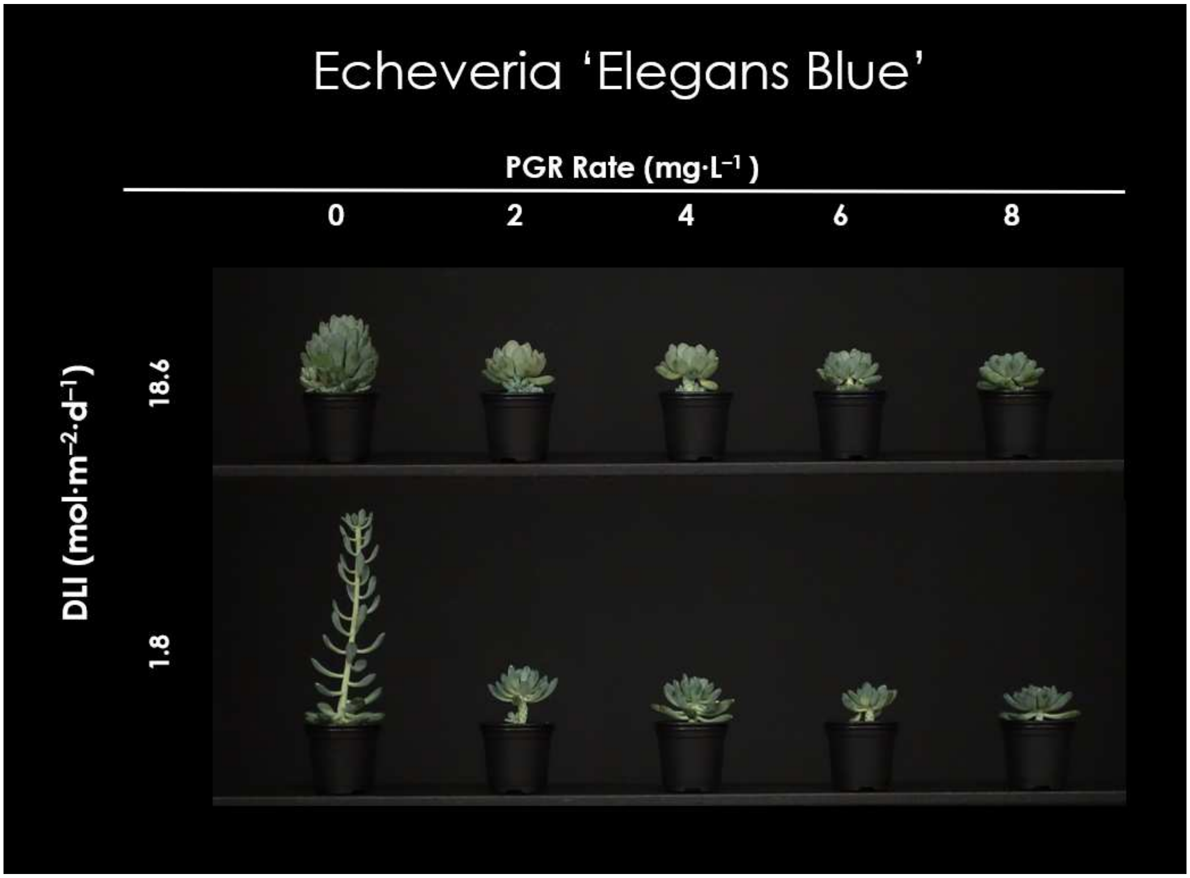


Figure II-4. *Echeveria* 'Elegans Blue' treated with a substrate drench of 0, 2, 4, 6, and 8 $mg \cdot L^{-1}$ paclobutrazol and grown under a low (1.8 $mol \cdot m^{-2} \cdot d^{-1}$) or high DLI (18.6 $mol \cdot m^{-2} \cdot d^{-1}$).



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SECTION IV

High day and night temperatures, but not the photosynthetic daily light integral, negatively influence growth and development of some succulent genera

Anthony J. Soster and Roberto G. Lopez*
Department of Horticulture, 1066 Bogue Street, Michigan State University, East Lansing, MI 48824-1325, USA

*Corresponding author. Tel.: +1 517-353-0342. E-mail address: rglopez@msu.edu (R.G. Lopez).

Abstract

Succulents have grown in popularity in recent years due, in part, to their diversity, drought tolerance, and unique leaves and colors. However, many genera are slow growing and research-based information is needed to determine if day, night, and mean daily temperature (MDT) interact with the photosynthetic daily light integral (DLI), and if these parameters can be manipulated to accelerate growth and development. Therefore, the objectives of this study were to 1) quantify how MDT and the DLI influence growth, morphology, and development of several succulent genera and species and 2) to develop models to predict responses to these environmental parameters. Shoot tip cuttings of tree houseleek (*Aeonium arboreum*) 'Nigrum', round-leafed navel-wort (*Cotyledon orbiculata*) 'Silver Peak', Mexican hens and chicks (*Echeveria hybrid*) 'Pollux', kalanchoe (*Kalanchoe villiosa*), panda plant (*K. tomentosa*), coral senecio (*Senecio fulgens*) 'Amke', and senecio (*Senecio ficoides*) 'Mount Everest' were received and grown in a greenhouse at 20 °C. After 83 to 137 d of propagation, plants were moved to one of five adjacent greenhouse compartments with day/night air temperature (MDT) set points of 34/28 (31), 31/25 (28), 28/22 (25), 25/19 (22), or 22/16 °C (19 °C), (12-h/12-h day/night). Three DLIs were created in each compartment by using no shade cloth or shade cloth to reduce radiation intensity by ~30% and ~50%. MDT and the DLI interacted to influence average leaf length and number, plant width and height, fresh and dry mass, and growth index of some genera and species. For instance, as MDT increased from 19.0 to 31.2 °C, *Aeonium* was 95% shorter when grown under a moderate DLI of 7.6 to 7.8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. However, at lower and higher DLIs, plants were more compact regardless of temperature. The leaf unfolding rate of *Echeveria* at an MDT of 28.2 °C increased by 20% as the DLI increased from 6.1 to 11.0 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, this trend was also observed at cooler temperatures. The fresh mass of *Senecio ficoides* had a quadratic increase from 98.9 to 143.7 g as temperature decreased from 30.9 to 21.9 °C, but as temperature further decreased from 21.9 to 18.8 °C, it decreased to 137.4 g. *Senecio fulgens* flowered only at MDTs $\leq$ 25 °C. Our research suggests there is a genera-specific optimum response for the variables we measured to MDT and DLI. In general, MDTs of 24.9 °C and DLIs of 6 to 8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ promoted growth of *Senecio ficoides*. Conversely, growth of *Senecio fulgens* was greatest at an MDT of 31.2 °C and DLIs of 5 to 6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, while cooler MDTs of 19 °C and DLIs of $\geq$11 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ promoted growth of *Aeonium arboreum*, *Cotyledon orbiculata*, *Echeveria hybrid*, *Kalanchoe villiosa* and *K. tomentosa*.

Keywords: *Aeonium*, DLI, *Echeveria*, greenhouse, *Kalanchoe*, mean daily temperature, potted plants, *Senecio*

Abbreviations: CAM, Crassulacean acid metabolism; DLI, daily light integral; HPS, high-pressure sodium; MDT, mean daily temperature; *PPFD*, photosynthetic photon flux density; T_b, base temperature; T_{max}, maximum temperature; T_{opt}, optimal temperature; U.S., United States

Introduction

The wholesale value of potted cacti and succulents sold in the United States (U.S.) totaled nearly $103 million USD in 2012, accounting for over 2% of total floriculture sales (USDA, 2014). In 2017, independent garden centers reported edible crops were the leading gardening trend (Garden Center Magazine, 2017); by 2019, succulents were the second-fastest growing trend in terms of sales; and 31% of garden centers grew succulents in their greenhouses (Garden Center Magazine, 2019). The popularity and demand for succulents is due, in part, to the intense colors and unique leaves, diversity, adaptability, drought tolerance, and ease of maintenance for consumers (Marquand and Valeris, 2020; Porkorny, 2020; Roach, 2020). They are predominantly used in dish gardens and containers, centerpieces, living walls, picture frames, topiaries, wreaths, bouquets, corsages, and as bedding plants and ground covers. The vast majority of commercially available succulents come from the stonecrop or houseleek family (*Crassulaceae*) in the genera *Aeonium*, *Cotyledon*, *Crassula*, *Echeveria*, *Graptopetalum*, *Kalanchoe*, *Pachyveria*, *Sedum*, and *Sempervivum* (Nam et al., 2016).

Generally, most succulents in *Crassulaceae* are believed to exclusively utilize Crassulacean acid metabolism (CAM) photosynthesis (Ting, 1985) and are often slow growing. However, suggesting all succulents exclusively use CAM is an oversimplification (Ranson and Thomas, 1960). Cushman (2001) suggested CAM photosynthesis is a facultative or inducible trait in the *Aizoaceae*, *Crassulaceae*, *Portulaceae*, and *Vitaceae* families. Thus, some plants transition from C_3-to-CAM; C_3 under abundant water availability, switching to CAM under drought conditions (Holtum et al., 2017; Winter and Holtum, 2017; von Willert et al., 1985). Water deficit is not the only trigger for facultative CAM plants; environmental conditions such as temperature, radiation intensity, and humidity also play a role (Lüttge, 2000). For instance, *Mesembryanthemum crystallinum* can transition from C_3-to-CAM under high radiation intensities or changes in radiation quality, depending on salinity stress (Cockburn et al., 1996; Miszalski et al., 2001).

When grown in greenhouses, the production cycle of some succulent genera can be as long as 10 to 12 weeks (Dümmen Orange, 2018), and longer during winter months (Nam et al., 2016). However, controlled environment production information is limited on this diverse group of plants (Erwin et al., 2017). Much of the current body of knowledge related to succulent responses to radiation intensity focus on effects on overall plant growth. For example, under low photosynthetic daily light integrals (DLIs) succulents are generally larger compared to those grown under higher DLIs. In one study, height of *Echeveria agavoides* and *E. marcus* increased by 7% and 13%, respectively, as the DLI decreased from 7.6 to 1.7 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Cabahug et al., 2017). In a separate study, the height and diameter of *Sedeveria* 'Letizia' increased by 12% and 16%, respectively, when 120 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of supplemental lighting was provided, compared to plants that received 60 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Nam et al., 2016). Currey and Erwin (2011) reported plant height of *Kalanchoe* was influenced by species-specific interaction with the DLI. For instance, increasing the DLI from 4.3 to 17.2 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ inhibited, promoted, or had no effect on stem elongation, depending on the species. Additionally, as the DLI increased, flower number and dry mass for all species studied increased (Currey and Erwin, 2011).

Similar to other plants, radiation intensity influences the accumulation of anthocyanins in succulents (Cabahug et al., 2017; Cruz et al., 2012; Nam et al., 2016). For example, the petiole anthocyanin concentration of *Kalanchoe brasiliensis* and *K. pinnata* decreased from 1.7 to 1.1 mg/100 g when the radiation intensity was reduced from 70% to 25% of full sunlight, respectively (Cruz et al., 2012). However, anthocyanin concentrations in leaves remained relatively consistent regardless of radiation intensities (Cruz et al., 2012). Similarly, as the DLI increased from 1.8 to 7.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, anthocyanin concentration of *E. agavoides* and *E. marcus* in leaves increased from 0.28 to 0.93 mg/100 g, and 0.12 to 0.31 mg/100 g, respectively (Cabahug et al., 2017).

Mean daily temperature (MDT) is the primary environmental parameter that affects the rate of plant development (Blanchard and Runkle, 2011). Frequently, temperature is modeled as a quadratic function, where the base temperature (T_b) is the point at or below which no development occurs, above which development increases linearly to the optimum temperature (T_{opt}) (Adams et al., 1998; Blanchard and Runkle, 2011). At temperatures greater than the T_{opt}, the rate of development decreases to the maximum temperature (T_{max}) (Adams et al., 1998; Blanchard and Runkle, 2011).

The T_{opt} of some succulents can be relatively high; in the case of *Aloe spp*. 'Firebird', *Haworthia fasciata*, and *Portulacaria afra variegata* the T_{opt} is >28 °C (Erwin et al., 2017). This is intuitive as plants utilizing CAM or C_4 photosynthesis concentrate carbon dioxide near Rubisco resulting in a suppression of photorespiration, a detrimental process that increases with increasing temperature (De la Barrera and Smith, 2009). The subsequent suppression of photorespiration can result in a higher T_{opt} of some CAM and C_4 plants (De la Barrera and Smith, 2009). Most studies conducted on cacti, succulents, and foliage plants have focused on developmental responses to increasing temperature. For instance, leaf unfolding of *Zamioculcas zamiifolia* was most rapid at MDTs of 29 and 32 °C and led to marketable plants after 6-8 months; while leaf unfolding was delayed at temperatures <26 °C (Lopez et al., 2009). *Schlumbergera truncata* 'Eva' grown at 24 °C flowered after 43 d, but at MDT of 12 °C, time to flower increased to 113 d (Larsen et al., 1998). Additionally, flower bud size decreased with increasing temperature. However, the temperatures investigated by Larsen et al. (1998) did not exceed 24 °C and did not find a temperature at which development began to slow. Excessively high temperatures can have detrimental effects on plant development (Bita and Gerats, 2013). For instance, the most rapid leaf unfolding of *Aeonium percarneum* 'Kiwi' occurred at MDTs from 10 to 22 °C and decreased at 28 °C (Erwin et al., 2017). Additionally, MDTs of 28 °C resulted in the death of *Crassula arborescens* 'Silver Dollar', *Sempervivum calcareum* 'Sir William Lawrence', and *Sedum burrito*, while *Gasteraloe hybrida* 'Green Ice' and *Echeveria* *hybrida* 'Lola' showed no change in leaf unfolding rate across MDTs of 10 to 28 °C (Erwin et al., 2017). While utilizing T_{opt} of a plant as a guide for hastening production times, it may also be necessary to provide a cooling period to plants in order to break dormancy or to simulate large temperature swings experienced in desert climates or through the changing of seasons. Some plants, such as *Echinopsis hybrida* 'Rose Quartz', require a cooling period of at least 4 weeks at 5 °C to break dormancy and initiate flowers (Erwin et al., 2016).

While DLI and temperature individually impact growth, morphology, and development, the interaction of these factors is important for understanding how plants respond to dynamic environmental conditions. For instance, Pramuk and Runkle (2005) reported MDT and DLI interacted to influence the development rate of *Impatiens walleriana*. Under DLIs <15 $mol \cdot m^{-2} \cdot d^{-1}$, an increase in MDT led to a decrease in time to flower; while under DLIs >15 $mol \cdot m^{-2} \cdot d^{-1}$, MDT played a less important role in floral development (Pramuk and Runkle, 2005). Therefore, models considering various environmental parameters are needed to optimize growth and development for crops that have long production times.

To our knowledge, there is no published work investigating the interaction of DLI and high to moderate MDT and day and night temperatures on succulent growth and development. Therefore, the objectives of this study were to 1) quantify the effects of DLI, high to moderate MDT and day and night temperatures on growth and development of several common genera and species of succulents and 2) develop models to predict growth and development of these crops under various environmental conditions.

Materials and methods

Cuttings of tree houseleek (*Aeonium arboreum*) 'Nigrum' (Rep. 1 only), round-leafed navel-wort (*Cotyledon orbiculata*) 'Silver Peak', Mexican hens and chicks (*Echeveria hybrid*) 'Pollux', kalanchoe (*Kalanchoe villiosa*), panda plant (*K. tomentosa*), coral senecio (*Senecio fulgens*) 'Amke' (Rep. 1 only), and senecio (*Senecio ficoides*) 'Mount Everest' (Rep. 2 only) were received on 09 July 2019 for Rep. 1 and 23 June 2020, 30 June 2020, and 03 July 2020 for Rep. 2 (Dümmen Orange NA, Inc., Columbus, OH; Mast Young Plants, Grand Rapids, MI). The following day, cuttings were inserted into 18-01 cell packs (373-mL) (East Jordan Plastics Inc., East Jordan, MI), with a mixture of (by volume) 75% commercial soilless media, containing 70% peat moss, 21% perlite, and 9% vermiculite medium (Suremix; Michigan Grower Products Inc., Galesburg, MI), and 25% perlite (Coarse Perlite; Perlite Vermiculite Packaging Industries Inc., North Bloomfield, OH). A foliar spray of indole-3-butyric acid (Advocate; Fine Americas, Inc., Walnut Creek, CA) and a surfactant (Capsil; Aquatrols, Paulsboro, NJ) at a concentration of 75 $\text{mg}\cdot\text{L}^{-1}$ and a volume of 0.2 $\text{L}\cdot\text{m}^{-2}$ was applied to the cuttings. Cuttings were placed in a glass-glazed greenhouse at Michigan State University (East Lansing, MI; lat. 43° N) under a 16-h photoperiod maintained with high-pressure sodium (HPS) lamps (LR48877; P.L. Lighting, Beamsville, ON, Canada) that provided a photosynthetic photon flux density (*PPFD*) of 62.5 ± 5.4 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. An environmental control system (Priva Office version 725-3030; Priva North America, Vineland Station, ON, Canada) controlled exhaust fans, evaporative-pad cooling, radiant hot-water heating, and supplemental lighting. The greenhouse MDT was 23.0 ± 1.8 °C and 23.9 ± 2.3 °C during Reps. 1 and 2, respectively, and the DLI was 12.5 ± 5.1 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ and 11.1 ± 5.0 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ during Reps. 1 and 2, respectively. Plants were irrigated as needed with reverse osmosis water blended with a water-soluble fertilizer (MSU Orchid RO Water

Special 13N–1.3P–12.5K; Greencare Fertilizers, Inc. , Kankakee, IL) containing (mg·L^{-1}): 125 N, 13 P, 121 K, 78 Ca, 19 Mg, 0.17 B, 0.43 Cu, 1.7 Fe, 0.85 Mn, 0.17 Mo, and 0.43 Zn.

After 63 to 70 d, plants were transplanted into 11-cm round (600-mL) containers (Dillen Products Inc., Middlefield, OH) filled with the aforementioned medium. Ten plants of each genus or species were randomly placed into one of five connecting glass-glazed greenhouse compartments with day/night air temperature set points (MDT) of 34/28 (31), 31/25 (28), 28/22 (25), 25/19 (22), or 22/16 (19°C) °C (12-h/12-h day/night). Three different DLIs were created in each compartment by using no shade cloth or shade cloth placed over individual benches that reduced radiation levels by ~30% and ~50% (Solaro 3215 D O FB and Solaro 5220 D O; Ludvig Svensson, Kinna, Sweden). Supplemental lighting was provided by HPS lamps which delivered a *PPFD* of ≈150 ± 5.4 μmol·m^{-2}·s^{-1} when the outdoor light intensity was below ≈440 μmol·m^{-2}·s^{-1}. In each greenhouse compartment, there was a shielded and aspirated 0.13-mm type E thermocouple (Omega Engineering, Stamford, CT) at crop height and an infrared thermocouple (OS36-01-T-80F; Omega Engineering) pointing at the leaf tissue to measure air MDT and leaf temperature, respectively. Additionally, on each bench, an enclosed thermistor (Model ST-100; Apogee Instruments, Inc., Logan, UT) was placed in the substrate to measure its temperature, and a quantum sensor (SQ-500-SS Full-Spectrum Quantum Sensor; Apogee Instruments, Logan, UT) placed at canopy height measured *PPFD*. A CR-1000 data-logger (Campbell Scientific, Logan, UT) collected the environmental data every 15 s and hourly means were recorded. The mean DLIs, air MDT, plant and substrate temperature ± SD are provided in Table 1. Plants were overhead fertigated with the above-mentioned water-soluble fertilizer once a week. Based on observation and weight of multiple containers within each treatment and block, plants were irrigated with reverse osmosis water between fertigation events to maintain similar substrate moisture and nutrition levels among all treatments.

After 9, 10, 10, 11, 12, or 13 weeks under treatments, plant height and diameter, length of the oldest leaf, number of newly unfolded leaves, node and branch number were recorded for *Echeveria*, *Cotyledon*, *Kalanchoe villiosa*, *Aeonium*, *K. tomentosa*, and *Senecio*, respectively. To provide an integrated measurement of plant size, the growth index was calculated according to Krug et al. (2010). Plants were deemed either reproductive or non-reproductive depending on the presence or absence of a visible inflorescence. Stem diameter, ≈1 cm below the lowest leaf, was measured using a digital caliper (41101 DigiMax; Wiha, Buchs, Switzerland) for Rep. 2. Internode length was calculated by dividing the plant height by the number of nodes. Plants were excised just above the medium surface and total shoot (stems and leaves) fresh mass was measured using a digital balance. Stems and leaves were placed into paper envelopes and placed inside a drying oven set at ≥70 °C for ≥6 d, after which dry mass was recorded.

The experiment was organized in a randomized complete-block design with a two-way factorial arrangement. Plants were blocked by temperature (five levels) and DLI (three levels) with 10 plants per treatment combination and were randomized. The experiment was performed twice over time and data were pooled by replication. Data were analyzed separately by species and genera with SAS version 9.4 (SAS Institute, Inc., Cary, NC) mixed model procedure (PROC MIXED) for analysis of variance. Data were regressed in SigmaPlot 14.5 (version 11.0, Systat Software, Inc., San Jose, CA).

Results

MDT and DLI interacted to affect average leaf length, height, and fresh and dry mass of *Aeonium* (Fig. 1). Generally, temperature had a more pronounced influence than DLI; increasing MDT resulted in a decrease in all the aforementioned parameters (Table 2; Fig. 1). For example, as MDT decreased from 31.2 to 19.0 °C and under a very low DLI of 4.8 to 6.2 $mol \cdot m^{-2} \cdot d^{-1}$, the fresh mass of *Aeonium* increased by over threefold (20 g) (Fig. 1B). Additionally, plants were 10.5 cm shorter after 11 weeks as MDT increased from 19.0 to 31.2 °C and under a low DLI of 7.6 to 7.8 $mol \cdot m^{-2} \cdot d^{-1}$ (Fig. 1C). Similarly, as the DLI increased from 7.6 to 11.4 $mol \cdot m^{-2} \cdot d^{-1}$ at an MDT of 19.0 °C, *Aeonium* plants were 16% shorter (3.4 cm). Average leaf length and dry mass followed similar trends (Figs. 1A and D).

The effects of DLI and MDT interacted to impact the height, width, and growth index of *Cotyledon* (Fig. 2). Within each MDT treatment, plants were more compact as DLI increased (Fig. 2A). For example, at an MDT of 18.8 °C, as the DLI increased from 7.3 to 13.2 $mol \cdot m^{-2} \cdot d^{-1}$, plants were 10.5% (2.7 cm) shorter (Fig. 2A). As MDT increased from 18.8 to 30.9 °C, height, width, and growth index of *Cotyledon* were reduced (Table 2; Fig. 2). For instance, average width and growth index were relatively constant from 13.9 to 12.9 cm and 18.2 to 18.3, respectively, as MDT increased from 18.8 to 24.9 °C and under a DLI of 13.2 to 14.3 $mol \cdot m^{-2} \cdot d^{-1}$. However, plants were more compact (10.3 and 11.9, respectively) at an MDT of 30.9 °C (Figs. 2B and C).

DLI and MDT interacted to influence the height and growth index of *Senecio fulgens* and *S. ficoides* (Table 2; Fig. 3). As MDT decreased from 30.9 to 18.8 °C, growth index of *S. ficoides* increased from 18.7 to 24.2 under low DLIs (6.3 to 7.3 $mol \cdot m^{-2} \cdot d^{-1}$) (Fig. 3A). Height of *S. ficoides* followed a similar trend (Fig. 3B). In contrast, as MDT increased from 19.0 to 24.9 °C, growth index and height of *S. fulgens* increased from 15.5 to 16.9 and 13.9 to 14.5 cm, respectively, when grown under a low DLI (4.8 to 6.2 mol·m^{-2}·d^{-1}) (Figs. 3C and D). A further increase in MDT to 31.2 °C resulted in the growth index and height increasing to 20.8 and 17.7 cm , respectively (Figs. 3C and D).

As the DLI increased from 4.8 to 11.4 mol·m^{-2}·d^{-1}, width and leaf length of *S. fulgens* decreased (Table 2; Figs. 4A and C). For example, plant width followed a quadratic response, the largest plants by width were those grown under a DLI of 4.8 mol·m^{-2}·d^{-1}, but as DLIs increased to 12.4 mol·m^{-2}·d^{-1}, width was reduced by 31% (from 14.5 to 10.0 cm) (Fig. 4A). Leaf length followed a linear reduction of 18% (0.9 cm) as the DLI increased from 4.8 to 12.4 mol·m^{-2}·d^{-1} (Fig. 4C). Similarly, as temperature increased from 18.8 to 30.9 °C, average plant width and dry mass of *S. ficoides* decreased linearly from 17.0 to 12.5 cm and 6.9 to 4.0 g, respectively (Table 2; Figs. 4B and D). Conversely, fresh mass had a quadratic response to temperature; increasing from 137 to 144 g as MDT increased from 18.8 to 21.9 °C; while decreasing to 99 g as MDT increased to 30.9 °C (Fig. 4E). *S. fulgens* was the only species to flower during the experiment and flowers only developed at temperatures ≤25 °C, with more developing under higher DLIs (data not shown).

DLI and temperature interacted to influence plant width, the number of unfolded leaves, and fresh mass of *Echeveria* after 63 d (Figs. 5A-C). For example, as MDT increased from 18.8 to 31.2 °C under a moderate DLI of 11.3 to 13.2 mol·m^{-2}·d^{-1}, the average width of *Echeveria* decreased by 31% from 15.8 to 10.8 cm (Fig. 5A). At an MDT of 28.2 °C, as the DLI increased from 6.1 to 11.0 mol·m^{-2}·d^{-1}, leaf number and fresh mass increased from 16 to 19 leaves and 127.7 to 164.3 g, respectively (Figs. 5B and C). Similarly, 17 leaves unfolded at an MDT of 31.2 °C, under a DLI of 11.4 mol·m^{-2}·d^{-1} (Fig. 5C).

DLI and MDT had an inverse effect on stem diameter and dry mass (Table 2; Fig. 6). For example, as the DLI increased from 6.3 to 14.3 $mol \cdot m^{-2} \cdot d^{-1}$, stem diameter and dry mass increased linearly from 11.5 to 13.0 cm and 5.1 to 7.9 g, respectively (Figs. 6A and C). In contrast, as MDT increased from 18.8 to 30.9 °C, stem diameter and dry mass decreased from 13.3 to 11.6 cm and 5.9 to 4.9 g, respectively (Figs. 6B and D). Similarly, *Echeveria* was 1.5 cm shorter as MDT increased from 18.9 to 31.1 °C (Fig. 6E).

Regardless of MDT, as the DLI increased from 4.8 to 14.3 $mol \cdot m^{-2} \cdot d^{-1}$, leaf number and dry mass of *K. villiosa* increased from 3.4 to 6.4 leaves (88%) and 3.8 to 7 g (84%), respectively (Figs. 7A and C). Conversely, as MDT increased from 18.8 to 30.9 °C, leaf number, dry and fresh mass were reduced by 27, 21, and 27%, respectively (Figs. 7B, D, and E.). DLI and MDT only interacted to effect final height of *K. villiosa*; however, the most profound changes occurred at the highest MDTs and lowest DLIs (Table 2; Fig. 5D). For example, as MDT increased from 18.8 to 31.2 °C, and the DLI increased from 7.3 to 11.4 $mol \cdot m^{-2} \cdot d^{-1}$, height increased by 13.6% (Fig. 5D).

As the DLI increased from 4.8 to 14.3 $mol \cdot m^{-2} \cdot d^{-1}$, *K. tomentosa* plants were 0.5 cm shorter and dry mass increased by 110% (Table 2; Fig. 8A and C). As MDT increased from 19 to 31.0 °C, height and dry mass decreased by 12 and 26%, respectively (Figs. 8B and D).

Discussion

Due to the prolonged time to produce marketable potted succulents of sufficient size and quality compared to most other floriculture crops, greenhouse growers are interested in hastening growth and development by manipulating environmental conditions (Erwin, 2009). It is well documented that temperature and DLI can have a profound impact on photosynthesis, plant growth, morphology, and development. However, limited research-based production information is currently available on how MDT and DLI interact to influence parameters such as leaf unfolding, flower initiation, and extension growth of popular succulents (Erwin et al., 2017).

Generally, the rate of development increases linearly as the MDT increases to a species-specific point, while increasing DLI increases biomass accumulation, growth, morphology, and yield. These two factors often interact to change the intensity of responses; species-specific responses often make trends difficult to observe. For instance, shoot dry mass of *Tagetes patula* 'Bonanza Yellow' increased fivefold as DLI increased from 8 to 28 $mol \cdot m^{-2} \cdot d^{-1}$ while temperature decreased from 26 to 14 °C (Moccaldi and Runkle, 2007). Additionally, as MDT increased from 15 to 28 °C, height of *Celosia argentea* 'Glory Mix' at flower increased from 17 to 27 cm under a DLI of 8 $mol \cdot m^{-2} \cdot d^{-1}$ (Pramuk and Runkle, 2005). In contrast, shoot dry mass of *Salvia splendens* 'Vista Red' was influenced to a greater extent by MDT compared to DLI; as MDT decreased from 24 to 18 °C shoot dry mass increased by 42% regardless of the DLI (Moccaldi and Runkle, 2007). Flower number of *Impatiens walleriana* 'Accent Red' was greatest at 16 °C and lowest at 28 °C. Similarly, flower number of *C. argentea* increased under cooler temperatures, except when DLIs were ≥22 $mol \cdot m^{-2} \cdot d^{-1}$ (Pramuk and Runkle, 2005). Succulents are morphologically different from bedding plants, as a result, we found similar trends with smaller differences. Similarly, to *S. splendens*, dry mass of *Aeonium* and *Senecio fulgens* was impacted to a greater extent by MDT compared to DLI. However, for *Echeveria* and *Kalanchoe villiosa* and *K. tomentosa* the DLI and MDT both influenced dry mass.

Many succulents exhibit xerophytic adaptations that have led to their proliferation in arid environments, in which water availability is limited (Das and Panda, 1995). For instance, popular genera such as *Aloe spp*. require high temperatures to unfold new leaves (Erwin et al., 2017). The

T_{opt} for leaf unfolding of *Aloe spp*. and *Aloe juvenna* is ≥28 °C; both of which are native to the lowlands, interior regions, or deserts of Southern Africa (Erwin et al., 2017). This has unfortunately perpetuated the misconception that all succulents have a high T_{opt} and require high DLIs. Furthermore, excessively high temperatures may actually lead to slow growth rates and even mortality in some genera and species. Musil et al. (2005) reported mortality of *Argyroderma pearsonii* increased by 53% when the temperature from ≈34.4 °C to ≈40 °C in its native environment of South Africa. Similarly, Erwin et al. (2017) reported *Sempervivum calcareum* and *Crassula arborescens* development ceased, and plants died at MDTs >28 °C.

We did not observe high mortality in any genera we investigated. However, we did record a reduction in leaf number, length and width, height, fresh and dry mass, growth index, and stem diameter of *Aeonium*, *Echeveria*, *Senecio ficoides*, and *Kalanchoe villiosa* and *K. tomentosa* when they were grown at day/night temperatures of 34/28 °C (MDT of 31 °C). This suggests the T_{opt} of these succulents is <31 °C. However, the growth index and height of *Senecio fulgens* increased at high temperatures. Under a low DLI of 7.6 to 8.9 $mol \cdot m^{-2} \cdot d^{-1}$ and as temperature increased from 19.0 to 31.2 °C, height of *Senecio fulgens* increased from 14.7 to 18.4 cm (Fig. 3B). Growth index of *Senecio fulgens* followed a similar trend (Fig. 3A). Interestingly, *Senecio ficoides* responded differently to high MDTs compared to *S. fulgens*, suggesting a species-specific response to temperature. Quality of *Senecio fulgens* began to decline when grown under the lowest DLIs, suggesting higher DLIs and warm temperatures produced the best quality plants.

The native range of *Echeveria* extends from the southwestern U.S. to Central and South America (Uhl, 1992). It is a pioneer plant, growing in arid, cool, high altitude outcroppings such as rocky cliffs and volcanic lava escarpments (Guillermo et al., 2019), both of which have substrates with little nutritional value or water holding capacities. Other genera, such as *Aloe*, *Gasteraloe*, *Haworthia*, and *Lithops*, are native to Southern Africa. Many of the species in this study are native to warm climates; *Cotyledon*, *Echeveria*, *Kalanchoe*, and *Senecio* are native to equatorial climates. However, *Aeonium* is native to temperate regions of Europe and the Canary Islands (Erwin et al., 2017; SANBI, 2021).

For genera native to Mexico and South Africa, such as *Beaucarnea recurvata*, *Anacampseros telephiastrum variegate* 'Sunrise', *Mammillaria gracilis fragilis* 'Arizona Snowcap', and *Haworthia fasciata*, the T_{opt} for leaf unfolding was ≥22 °C (Erwin et al., 2017). Lastly, some genera native to islands and mountainous regions, such as *Aeonium percarneum*, *Sempervivum calcareum* 'Sir William Lawrence', and *Adromischus cristatus* 'Key Lime Pie', have lower T_{opt} of ≈22, 22, and 16 °C, respectively (Erwin et al., 2017).

Much of the available flower induction information for succulents focuses on popular plants marketed as potted flowering plants (Lopez and Runkle, 2005; Newton and Runkle, 2009; Rohwer and Heins, 2007). For example, *Schlumbergera gaertneri* has been reported to require 8 weeks of vernalization ranging from 7.5 to 12.5 °C to initiate 100% flowering (Rohwer and Heins, 2007). Similarly, *Phalaenopsis spp.* require cool day temperatures for inflorescence initiation, while night temperatures seem to have little effect (Newton and Runkle, 2009). For instance, 100% of *Phalaenopsis* 'Mosella', *P*. 'Golden Treasure', and *P*. 'Explosion' initiated an inflorescence when grown at a constant 20 °C, compared to less than 10% when grown at 29 °C (Newton and Runkle, 2009). Similarly, both temperature and day length have been reported to influence flowering of cool-season orchids native to mountainous regions (Lopez and Runkle, 2006). For example, 90% of *Miltonia* Pam-pam ×*Miltonia* Alger 'Trinity' flowered when exposed to 14 °C and under a 9-h photoperiod, while temperatures ≥14 °C substantially reduced the flowering percentages regardless of photoperiod (Lopez and Runkle, 2006).

Night temperatures may also influence flowering of succulents. Coelho et al. (2018), demonstrated time to flower of *Kalanchoe prittwitzii* was reduced from 110 to 75 d as night temperatures increased from 6 to 18 °C. However, that increase in night temperature resulted in a reduction the inflorescence number decreasing from 13 to 7. Additionally, night temperature had no influence on time to flower of *K. longiflora* and *K. marmorata*, suggesting species-specific responses (Coelho et al., 2018). Research by Braun and Winkelmann, (2016) suggests that within the *Aizoaceae* family, there are genera-specific responses to temperature. For example, *Lampranthus spp.* produced 3 more flowers at 14 °C compared to plants grown under 20 °C. For instance, as MDT increased from 14 to 20 °C, flower number of *Delosperma* doubled from 4 to 8 flower buds per plant (Braun and Winklemann, 2016). However, *Lampranthus* produced 6 and 9 flowers per plant under a MDTs of 20 and 14 °C, respectively (Braun and Winklemann 2016). In the current study, *Senecio fulgens* was the only species to flower, with plants flowering at MDTs ≤25 °C. At day/night temperatures (MDT) of 28/22 °C (25 °C), 25/19 °C (22 °C), and 22/16 °C (19 °C) only 10, 57, and 23% of plants flowered (data not shown). As only one species flowered in our study, we were not able to quantify the influence of cool day and night temperatures on flower initiation and development. In a separate experiment conducted on *Echeveria* hybrids, we observed similar levels of incomplete flowering in response to light intensity and photoperiod (Soster, 2021). Flowering of *E.* ‘Jade Point’, ‘Apus’, and ‘Elegans Blue’ only occurred under day lengths ≤11-h, while flowering of *E.* ‘Canadian’ and ‘Topsy Turvy’ occurred under a wide range of photoperiods ranging from 9- to 16-h (Soster, 2021). Lastly, the greatest number of *E.* ‘Apus’ and ‘Jade Point’ flowered under a DLI of 12.8 mol·m^{-2}·d^{-1} (Soster, 2021). It is possible several factors, such as juvenility, temperature, photoperiod, and DLI, may interact to control flowering of succulents.

Our research provides evidence that MDT >25 °C are not necessary for all succulents. Growth and development of *Aeonium arboreum*, *Cotyledon orbiculata*, *Echeveria hybrid*, *Kalanchoe villiosa*, *K. tomentosa*, and *Senecio ficoides* is hastened at cool to moderate greenhouse temperatures of 19 to 25 °C and low to moderate DLIs of 6 to 12 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. Additional research on a wider range of day and night temperatures and succulent genera is necessary to elucidate the T_b, T_{opt}, and T_{max} for growth and development. Given that some cacti, such as *Echinopsis*, require a vernalization period to flower (Erwin et al., 2016), future experiments should focus on providing a cooling period to succulents that have flowers that appeal to consumers.

Not surprisingly, high DLIs resulted in greater dry mass, leaf unfolding, and stem diameter for some genera and plants were generally more compact. Additional research is needed to determine how DLIs >15 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ influence succulent production and economic yield curves need to be generated to compare the benefits of providing supplemental lighting. Based on our data, we were able to categorize genera based on their predicted T_{opt} and DLI: cool MDT of 19 °C and DLIs of $\geq$11 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (*Aeonium arboreum*, *Cotyledon orbiculata*, *Echeveria hybrid*, *Kalanchoe villiosa* and *K. tomentosa*), cool to moderate MDT of 25 °C and low DLIs of 6 to 8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (*Senecio ficoides*), and high MDT of 31 °C and high DLIs of $\geq$11 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (*S. fulgens*).

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APPENDIX

Table III- 1. Air (day/night) temperature set points, actual air mean daily temperature (MDT) (mean ± SD), day and night air, tissue, and root-zone temperature and daily light integral (DLI) for succulents grown at five different temperatures and under three different DLIs.

	Temperature (°C)						
Rep.	Air (day/night) set points	MDT	Day	Night	Tissue	Root-zone	DLI (mol·m^{-2}·d^{-1})
1	31 (34/28)	31.2 ± 1.4	34.3 ± 1.3	28.3 ± 1.8	32.9 ± 1.4	30.0 ± 1.7	11.4 ± 3.2
	-[x]	-	-	-	-	28.5 ± 1.7	7.8 ± 1.2
	-	-	-	-	-	29.6 ± 1.8	4.8 ± 1.8
	28 (31/25)	28.2 ± 1.4	32.2 ± 1.4	25.2 ± 1.8	29.9 ± 2.2	26.9 ± 1.7	11.0 ± 1.5
	-	-	-	-	-	26.9 ± 2.3	8.2 ± 3.0
	-	-	-	-	-	27.2 ± 1.8	6.1 ± 1.8
	25 (28/22)	25.0 ± 3.0	27.5 ± 3.0	22.6 ± 3.3	29.1 ± 2.6	25.1 ± 2.2	12.5 ± 1.2
	-	-	-	-	-	25.8 ± 2.8	8.7 ± 1.7
	-	-	-	-	-	23.2 ± 1.9	6.2 ± 3.2
	22 (25/19)	22.0 ± 1.2	25.2 ± 1.1	18.9 ± 2.9	24.1 ± 1.5	20.7 ± 2.2	12.4 ±1.8
	-	-	-	-	-	21.6 ± 1.5	8.9 ± 3.0
	-	-	-	-	-	24.9 ± 1.5	5.9 ± 1.2
	19 (22/16)	19.0 ± 1.3	22.0 ± 1.1	16.0 ± 2.2	22.8 ± 1.3	18.6 ± 2.0	11.4 ± 1.6
	-	-	-	-	-	19.2 ± 2.0	7.6 ± 3.0
	-	-	-	-	-	18.8 ± 2.2	6.2 ± 1.3
2	31 (34/28)	30.9 ± 0.7	33.3 ± 1.4	28.4 ± 0.8	32.0 ± 1.4	29.8 ± 0.8	13.4 ± 3.8
	-	-	-	-	-	29.1 ± 0.9	8.1 ± 2.0
	-	-	-	-	-	29.2 ± 0.8	6.3 ± 1.3
	28 (31/25)	27.8 ± 1.4	30.3 ± 2.2	25.4 ± 0.8	29.1 ± 1.8	-[y]	12.8 ± 2.9
	-	-	-	-	-	27.1 ± 1.2	10.0 ± 3.2
	-	-	-	-	-	26.3 ± 1.3	6.4 ± 1.7
	25 (28/22)	24.9 ± 1.1	27.3 ± 1.4	22.6 ± 1.1	28.9 ± 1.7	23.9 ± 1.6	14.3 ± 5.2
	-	-	-	-	-	24.0 ± 0.9	11.5 ± 2.5
	-	-	-	-	-	25.1 ± 1.6	7.2 ± 2.4
	22 (25/19)	21.9 ± 1.7[y]	24.5 ±1.6[y]	19.4 ± 2.0[y]	25.5 ± 2.2	22.3 ± 1.5	11.8 ± 2.2
	-	-	-	-	-	20.5 ± 2.0	9.2 ± 3.1
	-	-	-	-	-	21.2 ± 1.5[y]	7.9 ± 2.3
	19 (22/16)	18.8 ± 2.6	24.5 ± 3.1	16.2 ± 2.4	21.9 ± 3.2	16.6 ± 4.7	13.2 ± 5.2
	-	-	-	-	-	18.0 ± 2.0	9.0 ± 2.3
	-	-	-	-	-	17.5 ± 4.7	7.3 ± 2.1

[x] Air temperature recorded in one location in the greenhouse

[y] Data not collected

Table III-2. Regression equations, and R^2 values for average leaf length, width, height, leaf number, fresh and dry mass, growth index, and stem diameter of seven succulents in response to mean daily temperature (MDT; °C) and daily light integral (DLI; $\text{mol·m}^{-2}\text{·d}^{-1}$). All models are in the form of: $f = y0 + a*MDT + b*DLI + c*MDT^2 + d*DLI^2 + e*MDT*DLI$.

Parameter	y0	(a)MDT	(b) DLI	(c) MDT^2	(d) DLI^2	(e) MDT*DLI	R^2
Aeonium							
Leaf length		0.75	0.50	-0.04	-0.02		0.80
Dry mass		0.58	-0.06	-0.03			0.33
Fresh mass	116.36	4.74	-8.15	-0.28	0.13		0.72
Height	63.49	1.46	-3.82	-0.09	0.06		0.79
Cotyledon							
Height		-2.44	3.44	0.06	-0.09	0.04	0.55
Width	19.23	-2.20	0.73	0.07	-0.03	0.02	0.41
Growth index	13.00	-2.42	1.85	0.07	-0.05	0.03	0.53
Echeveria							
Dry mass	8.35	-0.11					0.11
Dry mass	4.03		0.19				0.13
Height	15.46	-0.07					0.08
Width		-0.13	1.51	-0.03			0.19
Leaf number		0.22	1.79		-0.04		0.40
Fresh mass		4.43	18.51		-0.48		0.24
Stem diameter	10.73		0.20				0.10
Stem diameter	16.01	-0.13					0.12
Kalanchoe tomentosa							
Leaf length	18.05	-0.30					0.04
Dry mass	3.20		0.24				0.19
Height	20.56		-0.16				0.07
Height	23.51	-0.18					0.24
Kalanchoe villiosa							
Dry mass	4.26		0.15				0.08
Dry mass	8.80	-0.13					0.16

Table III-2 (cont'd)

Height	29.20	-0.99	-0.25	0.03		0.01	0.25
Leaf number	4.30		0.14				0.10
Leaf number	8.40	-0.11					0.18
Fresh mass	139.90	-2.24					0.22
Senecio ficoides							
Width	22.85	-0.33					
Dry mass	11.65	-0.23					0.53
Height		-1.00	2.74		-0.07	0.03	0.65
Fresh mass	-176.44	28.68		-0.64			0.36
Growth index		-2.44	4.08		-0.11	0.08	0.53
Senecio fulgens							
Width	19.14		-1.49		0.06		0.38
Leaf length	5.52		-0.14				0.12
Growth index	17.57	-1.55	0.19	0.06			0.60
Height	11.91	-0.44	0.35				0.59

Figure III-1. Effects of mean daily temperature (MDT) and daily light integral (DLI) on average leaf length (A), fresh mass (B), height (C), and dry mass (D) of *Aeonium*.

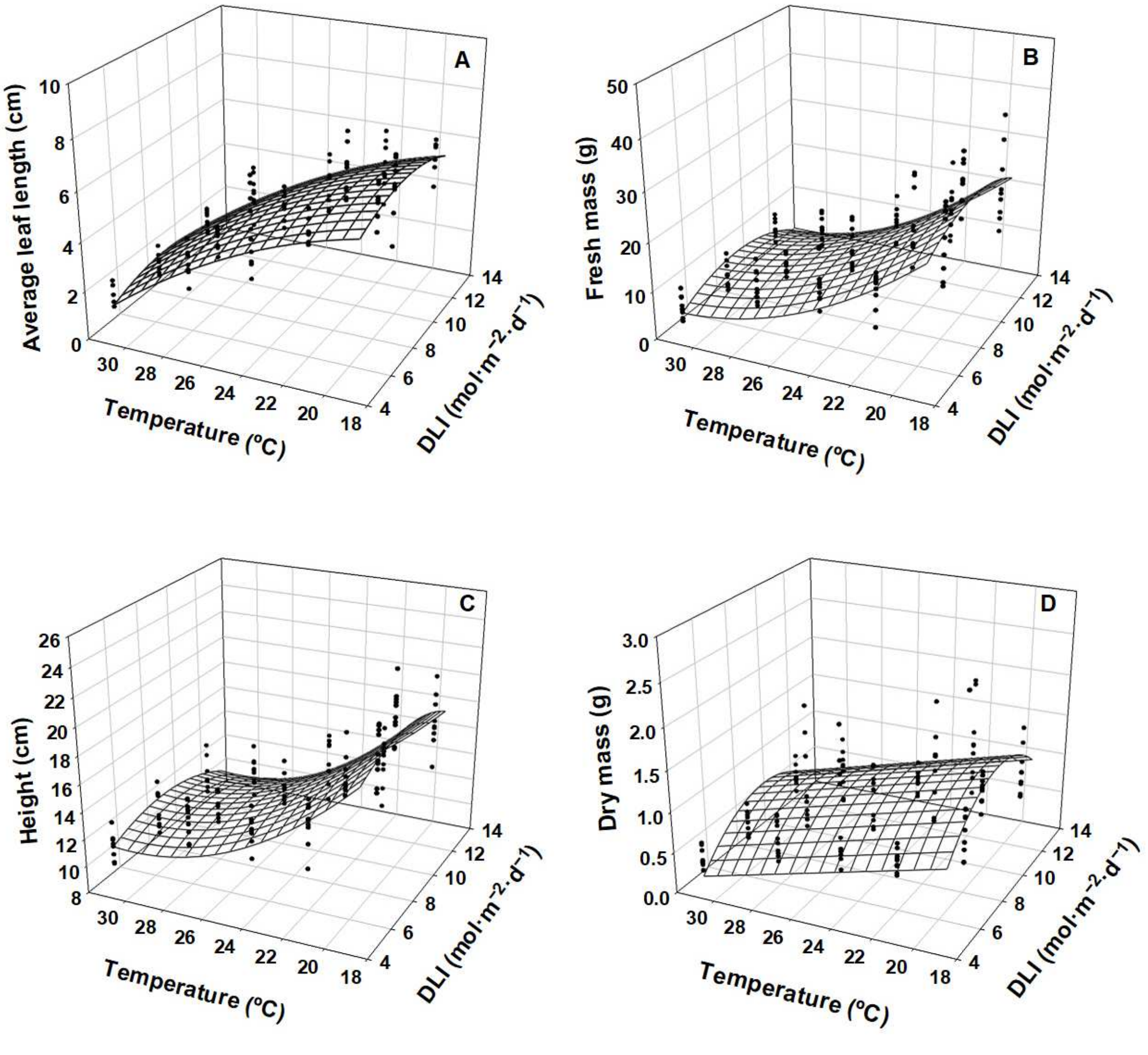


Figure III-2. Effect of mean daily temperature (MDT) and daily light integral (DLI) effects on height (A), width (B), and growth index (C) of *Cotyledon*.

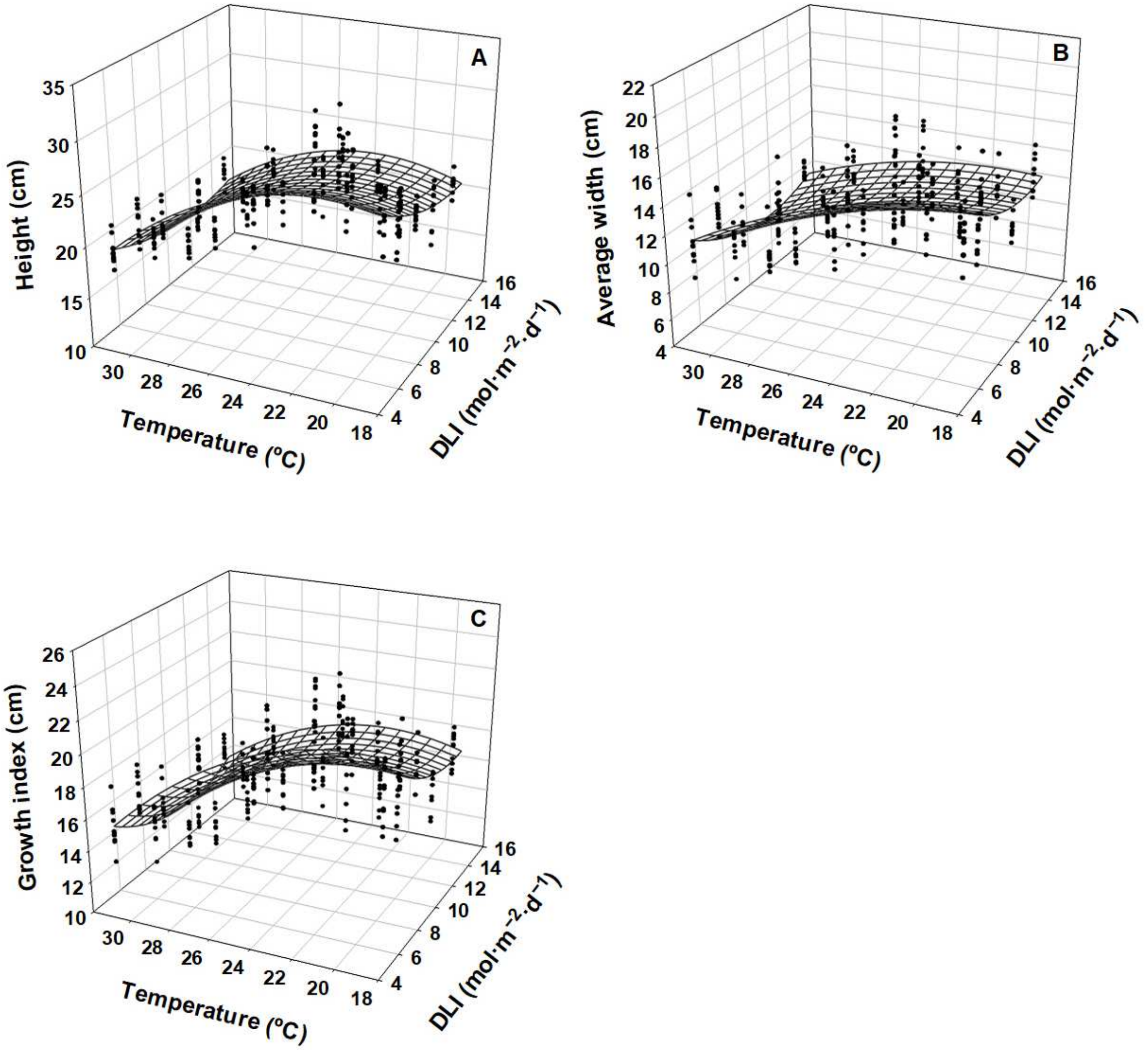


Figure III-3. Effect of mean daily temperature (MDT) and daily light integral (DLI) on growth index (A), height (B) of *Senecio ficoides*, and growth index (C), and height (D) of *Senecio fulgens*.

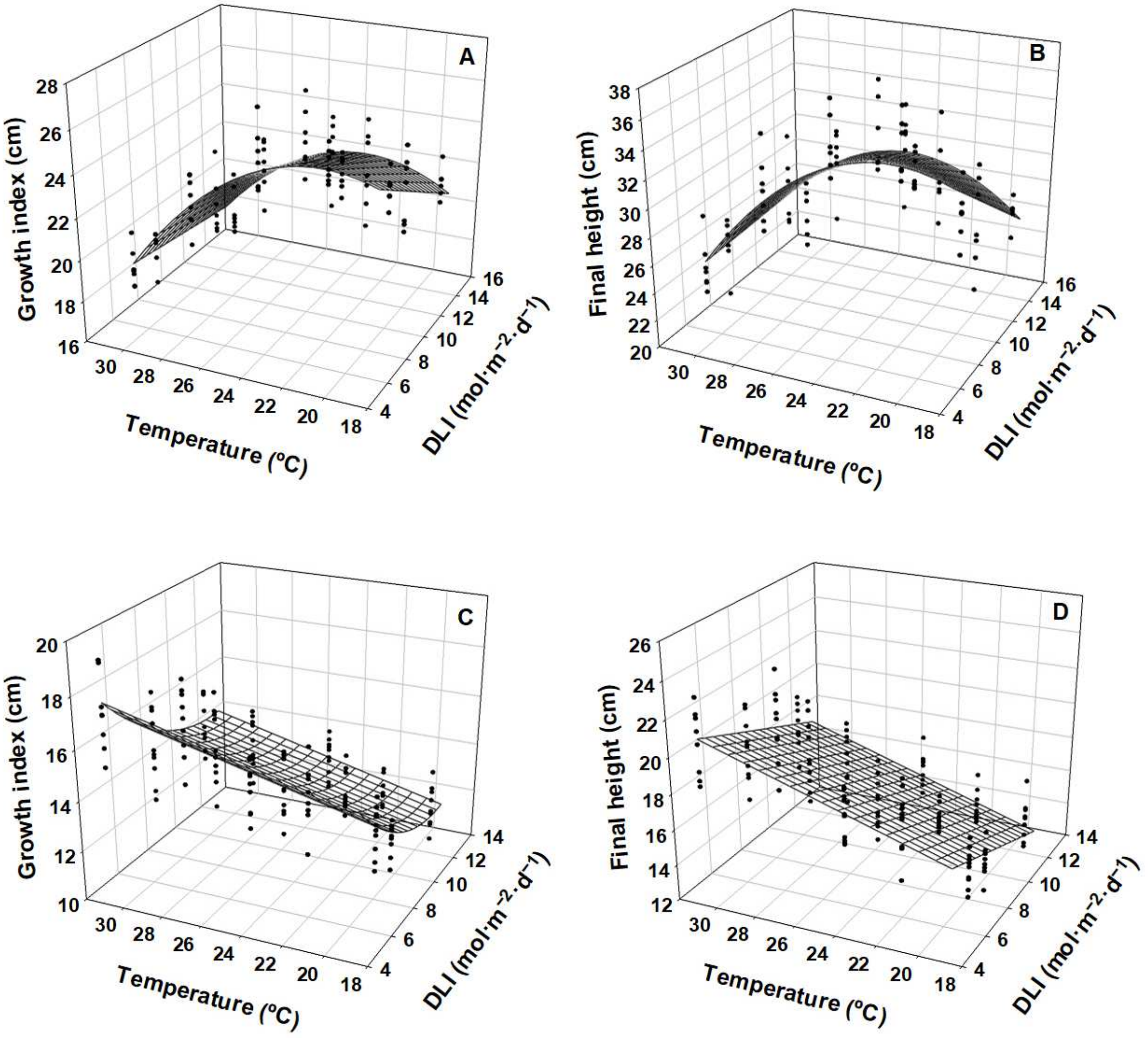


Figure III-4. Effect of daily light integral (DLI) on average plant width (A) and leaf length (C) of *Senecio ficoides* and of mean daily temperature (MDT) on average plant width (B), dry mass (D), and fresh mass (E) of *Senecio fulgens*.

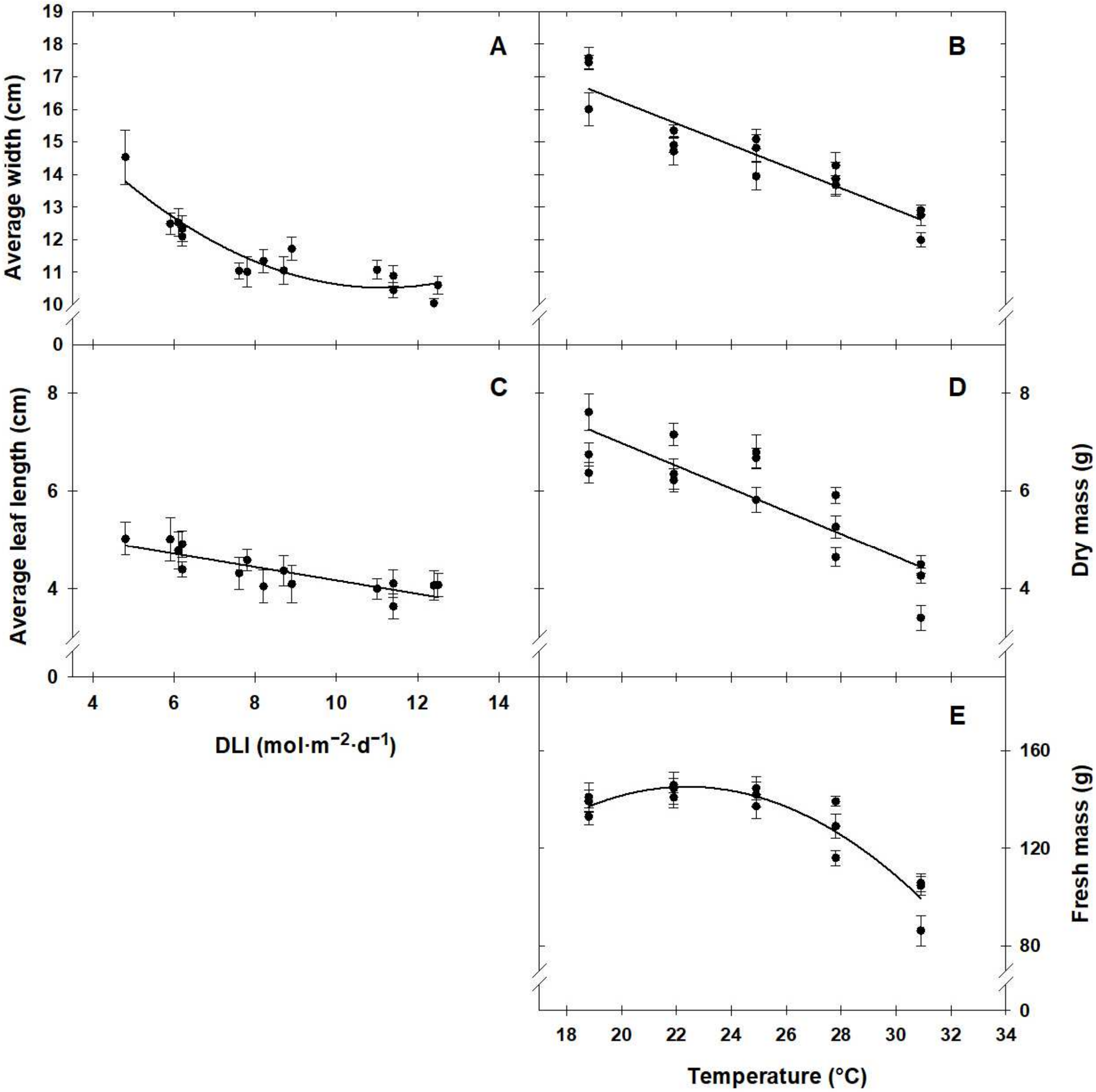


Figure III-5. Effect of mean daily temperature (MDT) and daily light integral (DLI) on average width (A), leaf number (B), fresh mass (C) of *Echeveria* and height of *Kalanchoe villiosa* (D).

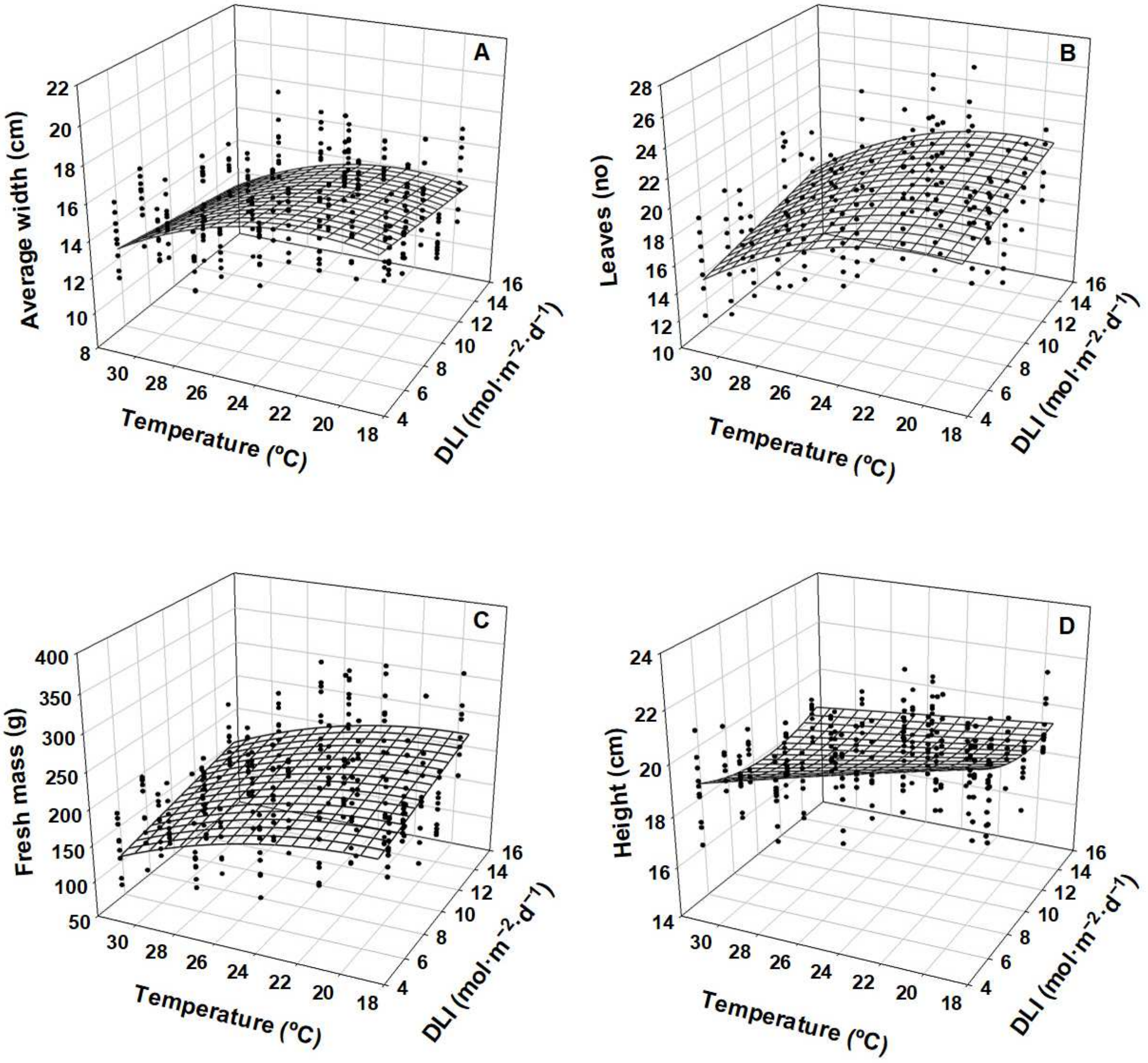


Figure III- 6. Effect of daily light integral (DLI) on stem diameter (A) and dry mass (C) and mean daily temperature (MDT) on stem diameter (B), dry mass (D), height (E) of *Echeveria*.

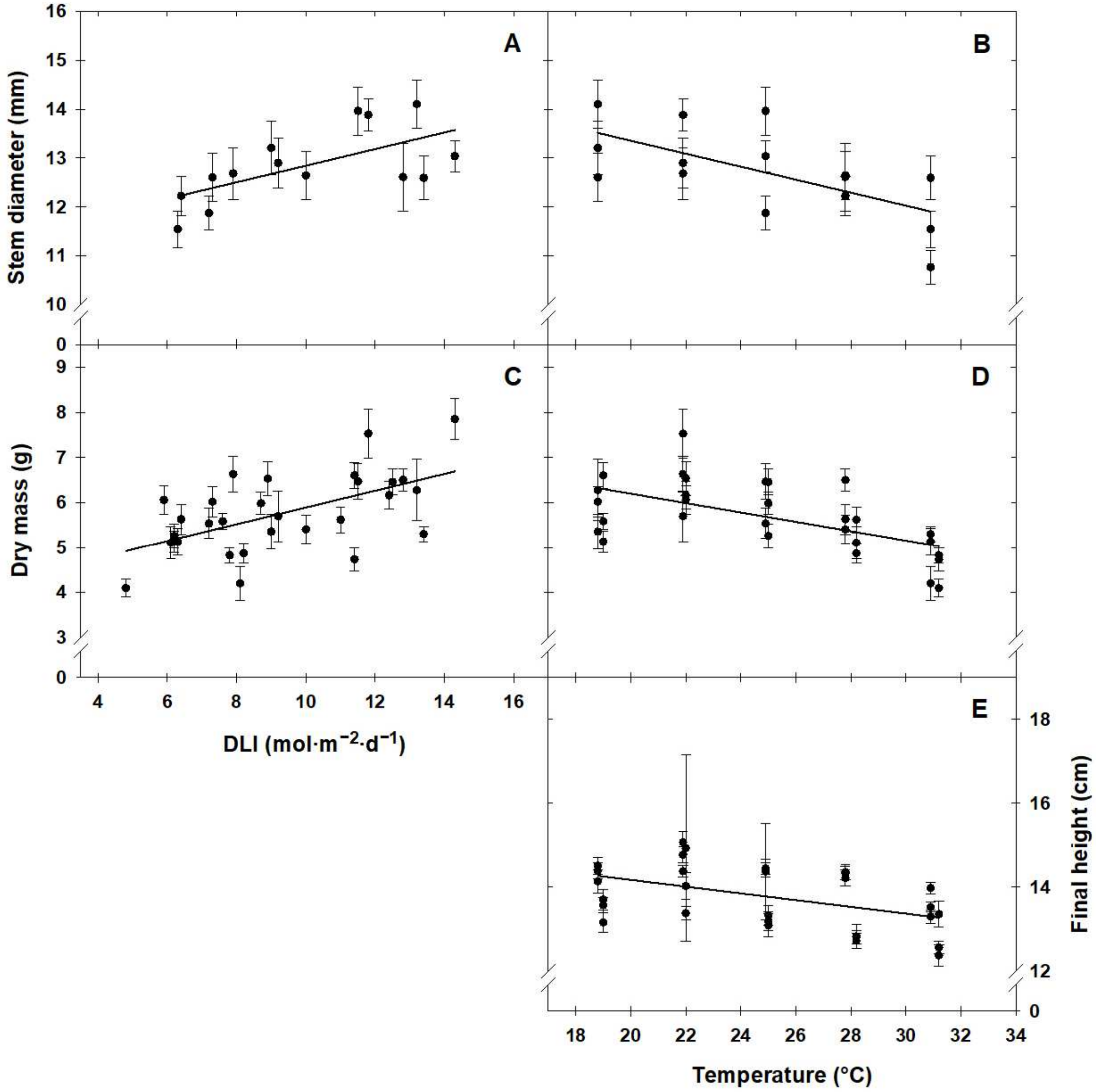


Figure III-7. Effect of daily light integral (DLI) on leaf number (A) and dry mass (C) and mean daily temperature (MDT) on leaf number (B), dry mass (D), and fresh mass (E) of *Kalanchoe villiosa*.

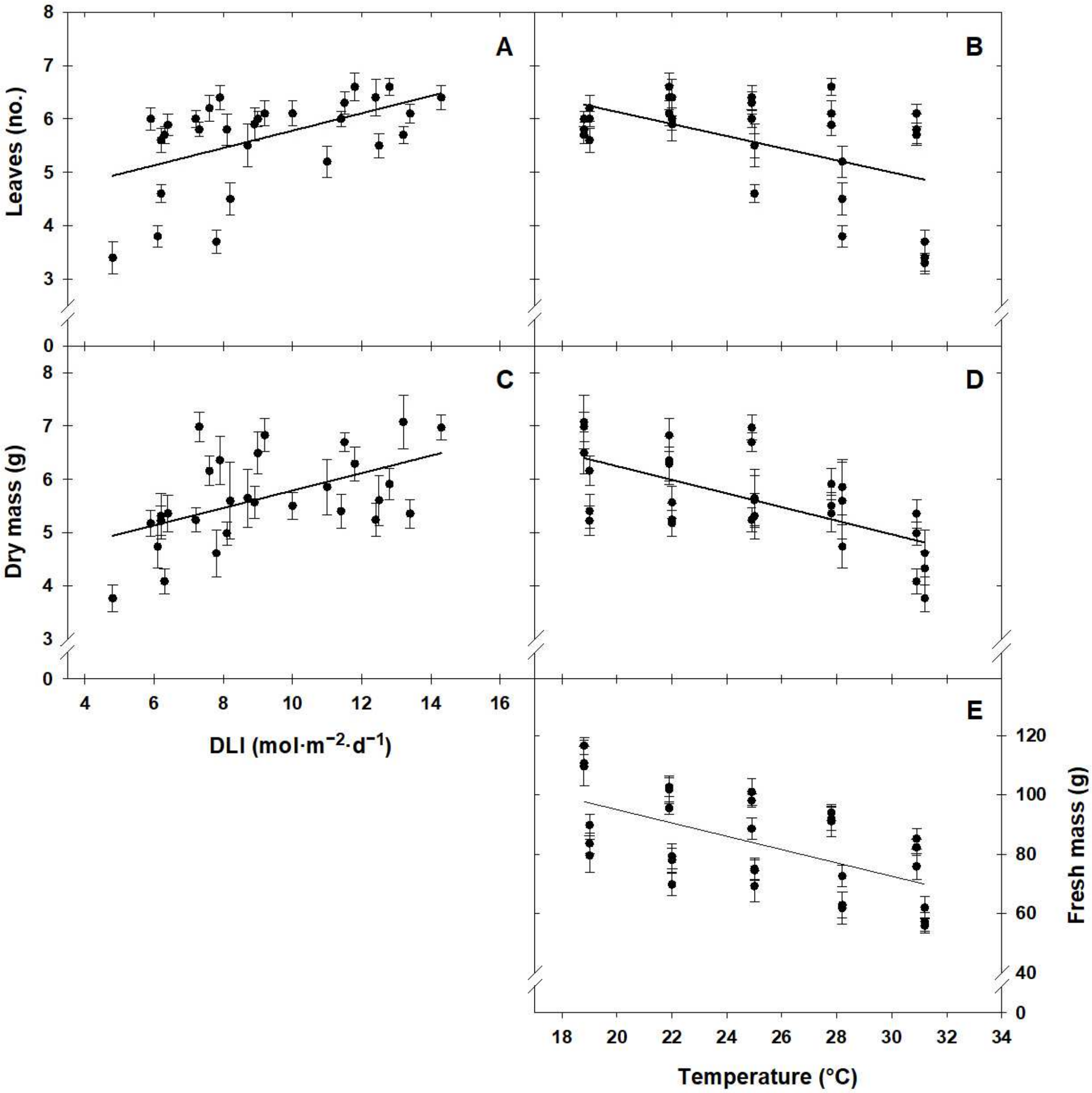


Figure III-8. Effect of daily light integral (DLI) on final height (A) and dry mass (C) and mean daily temperature (MDT) on height (B) and leaf length (D) of *Kalanchoe tomentosa.*

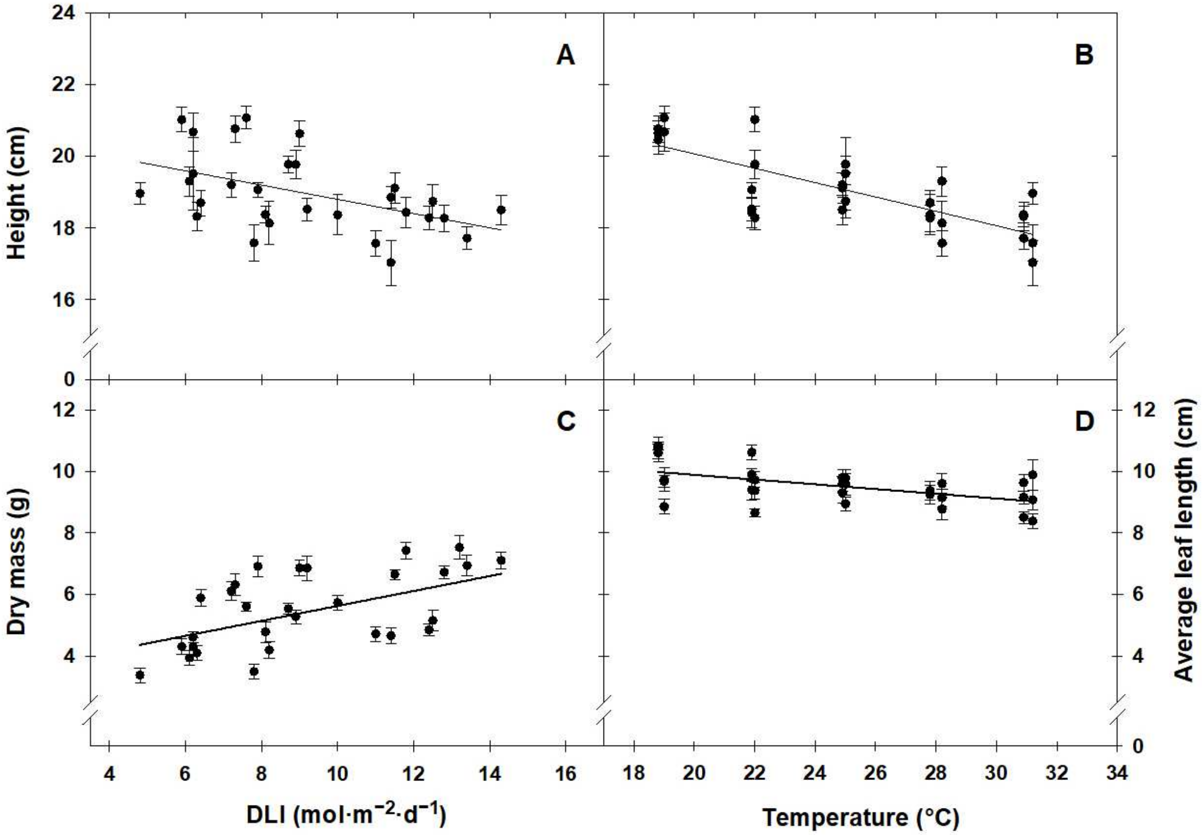
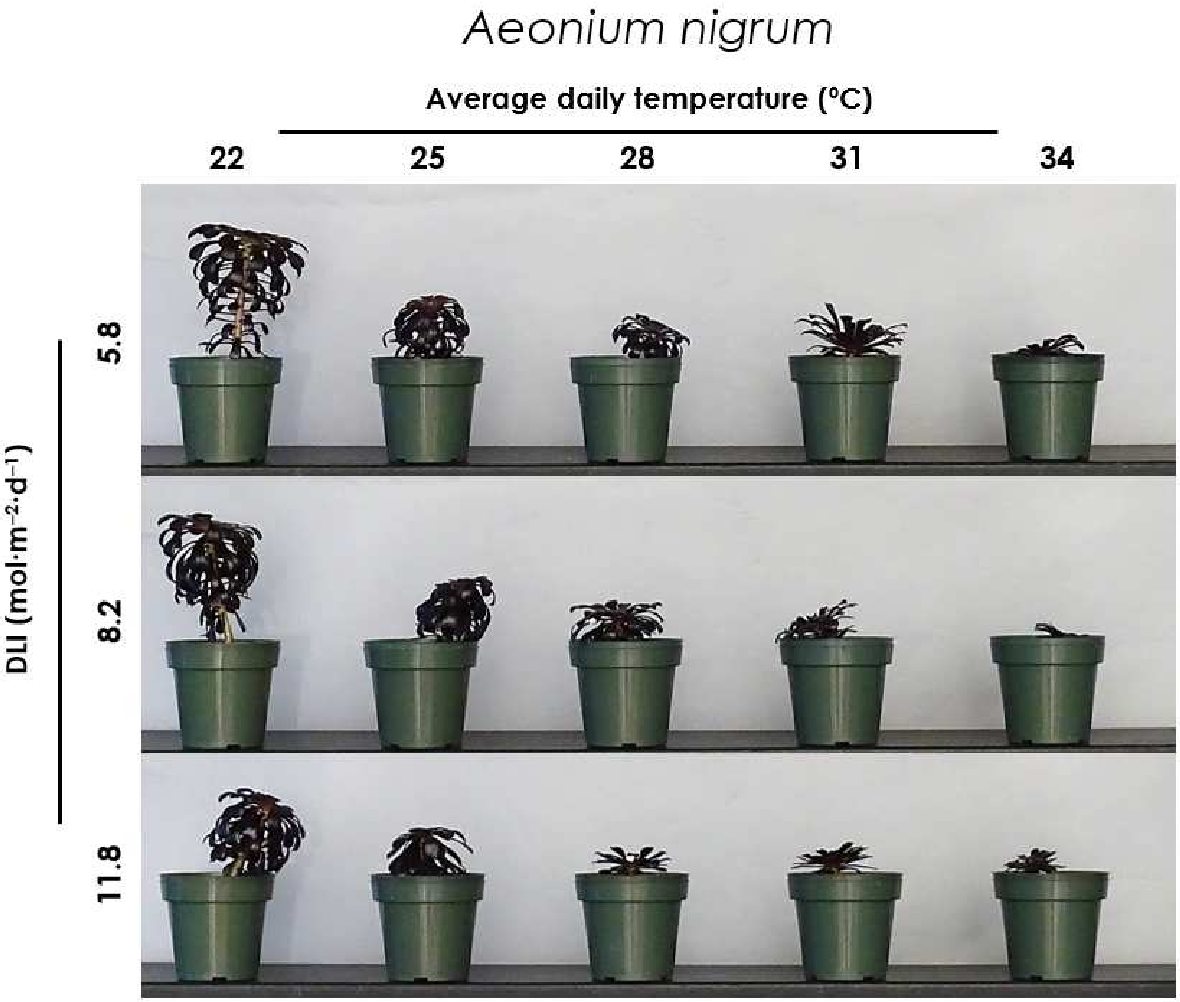


Figure III- 9. Effects of daily light integral (DLI) and mean daily temperature (MDT) on the growth and morphology of *Aeonium nigrum*.



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