

Temperature Impacts Cactus and Succulent Development Rate

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SUMMARY. One cactus and 17 succulent species/cultivars were grown at 10, 16, 22, or 28 °C (plant temperature) for 10 or 15 weeks. The change in leaf/tubercle number at each temperature (after 10 or 15 weeks) was determined, and leaf/tubercle-unfolding rate was calculated. ‘Jade Necklace’ kebab bush (*Crassula rupestris* ssp. *marnieriana*), ‘Lola’ echeveria (*Echeveria*), ‘Green Ice’ gasteraloe (*Gasteraloe*), and lithops (*Lithops* species) leaf-unfolding rate per day was unaffected by temperature. Leaf-unfolding rate per day increased as temperature increased from 10 to 16 °C on ‘Firebird’ aloe (*Aloe*), ‘Key Lime Pie’ adromischus (*Adromischus cristatus*), prostrate rainbow bush (*Portulacaria afra variegata*), burro’s tail (*Sedum burrito*), and ‘Sir William Lawrence’ houseleek (*Sempervivum calcareum*). Leaf-unfolding rate per day increased as temperature increased from 10 to 22 °C on mesquite agave (*Agave parryi truncata*), ‘Firebird’ aloe, Sunrise anacampseros (*Anacampseros telephiastrum variegata*), ponytail palm (*Beaucarnea recurvata*), subsessilis echeveria (*Echeveria subsessilis*), zebra plant (*Haworthia fasciata*), prostrate rainbow bush, burro’s tail and ‘Sir William Lawrence’ houseleek. Increasing temperature from 22 to 28 °C decreased ‘Kiwi’ tree houseleek (*Aeonium percarneum*) leaf-unfolding rate per day, increased ‘Firebird’ aloe and tiger tooth aloe (*Aloe juvenna*) leaf-unfolding rate, and resulted in shoot tip death on burro’s tail, and plant death of ‘Sir William Lawrence’ houseleek and ‘Silver Dollar’ jade (*Crassula arborescens*). The cactus, ‘Arizona Snowcap’ mammillaria (*Mammillaria gracilis fragilis*), tubercle-unfolding rate per day increased as temperature increased from 16 to 28 °C. Taken together, temperature (10 to 28 °C) effects on development rate were species specific and related to the indigenous environment of a species.

Interest in cacti and succulents as ornamental-potted and landscape plants has increased recently. Cacti and succulents can have ornamental foliage, or spines, unique forms and occasionally showy flowers. Cacti and succulents originate from a variety of climates (temperate, tropical, desert) but are similar in that each environment has periodic or prolonged drought (Anderson, 2001; Bailey, 1976).

Temperature effects on development rate are often quantified by

assessing the impact of temperature on leaf unfolding over time. In general, leaf-unfolding rate per day (development rate) increases as average daily temperature increases within a limited temperature range (Roberts and Summerfield, 1987; Vaid and Runkle, 2013). There is little or no information on how temperature affects development rate of many commercially grown cacti and succulents. Succulents and cacti differ in indigenous habitat, which differ in temperature, and how temperature impacts development rate of each species may differ. Understanding how temperature affects cacti and succulent development rate would facilitate greenhouse environment management and help identify geographic locations to successfully produce and schedule each crop. The objective of

research summarized here was to determine temperature effects (10 to 28 °C) on cacti and succulent development rate to determine appropriate greenhouse temperatures and/or optimal geographic locations to produce these crops.

Materials and methods

Three hundred sixty plants of 17 two-year-old vegetatively propagated succulent plant types and one sexually propagated cactus species grown in three 1/2-inch-diameter plastic pots in a soilless media were received from Altman Plants, Inc., Vista, CA [20 plants of each species/cultivar (Table 1)]. Plants were unpacked and acclimatized in a greenhouse for at least 2 weeks [22 ± 1 °C day/18 ± 1 °C night temperature; natural photoperiod (10 h); daily light integral (DLI) = 4.4 mol·m⁻²·d⁻¹]. Two hundred eighty-eight plants were selected for uniformity based on leaf number, plant height, and/or branch number (16 of each species/cultivar), and were then further divided into four groups of 18 plants each (one of each species per group). Each group was moved into one of four environmental growth chambers (over time) where air temperatures were managed in each to achieve a 10, 16, 22, or 28 °C plant temperature (mean of three different infrared thermometer brands across species). The uppermost “unfolded” (≥45° from the main stem axis) leaf (succulents) or tubercle (cactus) on each plant was marked using an indelible ink marker when plants were placed in chambers based on the angle of that leaf/tubercle to the main stem. Chamber irradiance and photoperiod were 300 μmol·m⁻²·s⁻¹ [75% wattage from fluorescent lamps and 25% from incandescent lamps (DLI = 12.96 mol·m⁻²·d⁻¹)] and 12 h, respectively, and chamber humidity was set to 40%. Plants were watered as needed (media at the bottom of the pot never dried) and were fertilized once weekly with a solution containing 250 ppm nitrogen from a 15N-2.2P-12.5K

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Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
2.54	inch(es)	cm	0.3937
1	ppm	mL·m ⁻³	1
(°F - 32) ÷ 1.8	°F	°C	(°C × 1.8) + 32

Table 1. Succulent and cactus plant material evaluated for variation in temperature effects [10 to 25 °C (50.0 to 77.0 °F)] on leaf/tubercle-unfolding rate per day and the indigenous habitat that each plant is from.

Plant	Indigenous habitat ^z
'Kiwi' tree houseleek	Canary Islands
Mescal agave	Southwest United States and Mexico
'Firebird' aloe	Southern Africa
Tiger tooth aloe	Southern Africa
Sunrise anacampseros	South Africa
'Key Lime Pie' adromischus	South Africa (mountains)
Ponytail palm	Texas and Mexico
'Silver Dollar' jade	Madagascar
'Jade Necklace' kebab bush	South Africa/Madagascar
'Lola' echeveria	Texas to Argentina
Subsessilis echeveria	Texas to Argentina
'Green Ice' gasteraloe	South Africa
Zebra plant	South Africa
Lithops	Western South Africa/Namibia
'Arizona Snowcap' mammillaria	Central Mexico
Prostrate rainbow bush	South Africa
Burro's tail	Eastern Mexico (mountains)
'Sir William Lawrence' houseleek	Europe, Morocco/west Asia

^zBailey (1976), Anderson (2001).

fertilizer (Excel 15-5-15 Cal-Mag; Everris, Marysville, OH). Plants were not leached to insure media fertility was similar between temperature treatments.

Nine succulent species/cultivars with more rapid leaf unfolding were removed from chambers after 10 weeks (greater than three leaves unfolded after 10 weeks). A second group of nine species/cultivars with a slower leaf/tubercle-unfolding rate (less than three leaves/tubercles unfolded after 10 weeks) was removed after 15 weeks. "Unfolded" leaf/tubercle number above the mark when plants were moved in was counted when plants were removed from chambers. The leaf/tubercle-unfolding rate per day for each plant was calculated by dividing the number of new leaves/tubercles unfolded in chambers by time in chambers (70 or 95 d). The experiment was organized in a completely randomized statistical design in a factorial arrangement with temperature and species/cultivar as the main factors. The experiment was replicated four times over time (one plant/replicate). Analysis of variance was conducted using SPSS [version 24; IBM Corp., Armonk, NY (Table 2)]. Regression analysis across temperatures (within a species) was also conducted (Table 2). The Tukey's honestly significant difference test

at $P \leq 0.05$ was employed for mean separation.

Results

How temperature affected development rate differed among species and cultivars (Table 2). Temperature (10 to 28 °C) did not affect development rate of 'Jade Necklace' kebab bush, 'Lola' echeveria, 'Green Ice' gasteraloe, and lithops (Table 2). In contrast, leaf-unfolding rate per day increased as temperature increased from 10 to 16 °C on 'Firebird' aloe, 'Key Lime Pie' adromischus, prostrate rainbow bush, burro's tail, and 'Sir William Lawrence' houseleek (Table 2). Leaf-unfolding rate per day increased when temperature increased from 10 to 22 °C on mescal agave, 'Firebird' aloe, Sunrise anacampseros, ponytail palm, subsessilis echeveria, zebra plant, prostrate rainbow bush, burro's tail, and 'Sir William Lawrence' houseleek (Table 2). 'Arizona Snowcap' mammillaria tubercle-unfolding rate increased as temperature increased from 16 to 28 °C (Table 2).

Increasing temperature from 22 to 28 °C decreased 'Kiwi' tree houseleek leaf-unfolding rate, but 'Firebird' aloe and tiger tooth aloe leaf-unfolding rate per day increased (Table 2). Although not significant, zebra plant and prostrate rainbow bush leaf-unfolding rate per day increased when

temperature increased from 22 to 28 °C (Table 2). The apical meristem of burro's tail died, and the entire plant of 'Sir William Lawrence' houseleek and 'Silver Dollar' jade died when temperature increased from 22 to 28 °C (Table 2).

Discussion

Intermediate temperature (similar to here) effects on development rate of some succulents and tropical cacti have been studied. *Kalanchoe* [*Kalanchoe blossfeldiana* (indigenous to Madagascar; Bailey, 1976)] time to flower decreased 19 d when temperature increased from 18 to 24 °C, but decreased only 2 d more when temperature was increased further from 24 to 26 °C (Carvalho et al., 2006). Thanksgiving cactus [*Schlumbergera truncata* (indigenous to Brazil; Bailey 1976)] days from flower induction to anthesis decreased from 100 to 52 d when average daily temperature increased from 12 to 20 °C and was unchanged when average daily temperature was further increased from 20 to 24 °C (Erwin et al., 1990). Maximum (64 to 71 °C) or minimum temperature (-22 to -5 °C) tolerance of desert cacti has been studied; however, there is little work on intermediate temperature effects on desert cacti development rate [as 'Arizona Snowcap' mammillaria here (Nobel and Bobich, 2002; Nobel and De la Barrera, 2003)].

There was considerable diversity in temperature effects on development rate of the cactus and succulents species/cultivars studied here (Table 2). In some cases, we could identify temperatures with the fastest leaf/tubercle-unfolding rate per day. For instance, since 'Kiwi' tree houseleek and 'Key Lime Pie' adromischus development rate increased as temperature increased from 10 to 22 °C and then decreased when temperature was further increased from 22 to 28 °C, we could elucidate that the highest leaf/tubercle-unfolding rate per day was at, or near, 22 °C (Table 2). Also, the temperature with the highest leaf/tubercle-unfolding rate for burro's tail, 'Sir William Lawrence' houseleek and 'Silver Dollar' jade development rate was <28 °C, as the apical meristem or the entire plant died when plants were grown at 28 °C (Table 2). Still other species/cultivars exhibited increased development rate when temperatures increased from 22 to 28 °C indicating that the temperature with

Table 2. Effect of plant temperature on leaves/tubercle unfolding per day and days to unfold three leaves/tubercles (three leaves divided by the leaf/tubercle-unfolding rate per day) of 17 succulent species/cultivars and one cactus species. Leaf and tubercle-unfolding rates were calculated after 10 (two decimals) or 15 weeks (three decimals). Regression analysis was conducted and the correlation between temperature and leaf-unfolding rate per day (r^2) was determined and the statistical significance of linear (L) and quadratic (Q) regression terms are reported below. The temperature range where the “most rapid leaf/tubercle unfolding” was determined was based on that temperature with the highest leaf/tubercle-unfolding rate per day and determining what mean leaf/tubercle-unfolding rates per day were different or not using Tukey’s honestly significant difference test (HSD).

Plant material	Plant temp (°C) ^z				r^2	Significance		Most rapid leaf unfolding (d)
	10	16	22	28		L	Q	
‘Kiwi’ tree houseleek	0.10 ab ^y	0.13 b	0.13 b	0.03 a	0.40	NS	*	10–22
	30 ^x	23	23	100				
Mescal agave	0.000 a	0.010 ab	0.012 b	0.010 ab	0.57	*	**	16–28
	—	300	250	300				
‘Firebird’ aloe	0.000 a	0.023 b	0.023 b	0.040 c	0.88	***	***	≥28
	—	130	130	75				
Tiger tooth aloe	0.03 a	0.07 ab	0.10 ab	0.12 c	0.83	***	***	≥28
	100	43	30	25				
Sunrise anacampseros	0.02 a	0.04 a	0.14 b	0.15 b	0.83	***	***	22–28
	150	75	21	20				
‘Key Lime Pie’ adromischus	0.11 a	0.21 b	0.13 ab	0.04 a	0.57	NS	**	16–22
	27	14	23	75				
Ponytail palm	0.010 a	0.019 a	0.073 b	0.071 b	0.87	***	***	22–28
	300	158	41	42				
‘Silver Dollar’ jade	0.019 a	0.028 a	0.019 a	Dead	0.34	NS	NS	— ^w
	158	107	158	—				
‘Jade Necklace’ kebab bush	0.08 a	0.12 a	0.13 a	0.09 a	0.18	NS	NS	—
	38	25	23	33				
‘Lola’ echeveria	0.14 a	0.18 a	0.18 a	0.13 a	0.28	NS	NS	—
	21	17	17	23				
Subsessilis echeveria	0.10 a	0.19 ab	0.27 b	0.16 ab	0.63	NS	**	16–28
	30	16	11	19				
‘Green Ice’ gasteraloe	0.007 a	0.009 a	0.017 a	0.017 a	0.28	NS	NS	—
	428	333	176	176				
Zebra plant	0.014 a	0.030 ab	0.059 bc	0.088 c	0.84	***	***	22–28
	214	100	51	34				
Lithops	0.004 a	0.029 a	0.021 a	0.036 a	0.35	NS	NS	—
	750	103	143	83				
‘Arizona Snowcap’ mammillaria	0.04 a	0.12 ab	0.11 ab	0.14 b	0.60	***	**	22–28
	75	25	27	21				
Prostrate rainbow bush	0.005 a	0.014 bc	0.033 bc	0.038 c	0.57	**	**	16–28
	600	214	91	79				
Burro’s tail	0.050 a	0.171 b	0.202 b	Dead tips	0.80	**	**	16–28
	60	18	15	—				
‘Sir William Lawrence’ houseleek	0.37 a	0.68 b	0.77 b	Dead	0.78	**	**	16–28
	8	4	4	—				
ANOVA ^x								
Species/cultivar	*							
Temperature	*							
Species/cultivar × temperature	***							

ANOVA = analysis of variance.

^z(1.8 × °C) + 32 = °F.

^yMeans (across temperatures) followed by different letters are significantly different based on Tukey’s HSD ($P \leq 0.05$).

^xTime to unfold three leaves calculated from the mean leaf-unfolding rate per day at each temperature.

^w“—” denotes no optima temperature determination for leaf/tubercle was possible as there was no significant temperature effect.

Denotes significance ($P \leq 0.05$) as determined by ANOVA; NS, *, **, *** nonsignificant at $P \leq 0.05$, 0.01, or 0.001, respectively. r^2 was also presented for reference.

the highest leaf/tubercle-unfolding rate per day of these species/cultivars was ≥28 °C (Table 2).

Species where development rate slowed when temperature increased from 22 to 28 °C are indigenous to

islands, mountains, or western Europe where more moderate temperatures may occur more than in tropical or

desert climates (Table 1). *Kalanchoe* reportedly has an optimal temperature at or near 24–26 °C (Carvalho et al., 2006); ‘Silver Dollar’ jade here (similar indigenous location as *Kalanchoe*) had a similar optimal temperature (Table 2). In contrast, species with optimal development rate temperatures ≥ 28 °C here (‘Firebird’ aloe, tiger tooth aloe, zebra plant, prostrate rainbow bush, and ‘Arizona Snowcap’ *mammillaria*) are indigenous to interior regions, lowlands, or deserts of South Africa, or central Mexico with warmer temperatures (Table 1). Future work on species from warm regions should include temperatures >28 °C to insure identification of optimal development rate temperatures.

We suspect burro’s tail, Sir William Lawrence houseleek, and ‘Silver Dollar’ jade tip or plant death observed here was related to warm night temperatures, as these plants are routinely exposed to day temperatures ≥ 28 °C in commercial production and the landscape and plants do not die (personal observation). High night temperatures, or night temperatures similar to day temperatures, could limit carbon dioxide (CO₂) uptake and result in carbohydrate limitation of growth, as CO₂ is taken up during the night on plants that exhibit crassulacean acid metabolism (CAM) as many cacti and succulents do. Prickly pear (*Opuntia ficus-indica*) maximum CO₂ uptake occurred at a 15 °C night temperature (Nobel and Bobich, 2002; Nobel and Hartsock, 1984). In contrast, the epiphytic cacti night blooming cereus (*Hylocereus undatus*) had an optimal night temperature for CO₂ uptake of 25 °C

(Raveh et al., 1995). Whether plants studied here photosynthesize exclusively via the CAM pathway is not known; however, future work should focus on night temperature limitation of photosynthesis as such inhibition may have occurred on other species here that did not exhibit shoot tip or plant death. High night temperatures may also limit growth of some species/cultivars in the landscape in warmer climates or in buildings without expressing obvious symptoms.

Research results reported here provide some insight and guidance on how cactus and succulent production time may be impacted when temperature is changed between 10 and 28 °C. For instance, calculated production time (three leaves divided by leaf-unfolding rate per day) to unfold three leaves at 22 °C was 130 d on ‘Firebird’ aloe, but was 75 d when plants were grown at 28 °C [55 d less time (Table 2)]. In contrast, ‘Key Lime Pie’ *adromischus* unfolded three leaves after 23 d when grown at 22 °C, but took 75 d to unfold three leaves when grown at 28 °C [53 d longer (Table 2)]. These data suggest that species/cultivars should be grouped by temperature development rate responses to insure greenhouse temperature management decisions or selection of outdoor production locations do not inadvertently increase production time.

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