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Elongation of *Hibiscus acetosella* Under Well-watered and Drought-stressed Conditions

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Abstract. **Controlling the elongation of ornamental plants is commonly needed for shipping and aesthetic purposes. Drought stress can be used to limit elongation, and is an environmentally friendly alternative to plant growth regulators (PGRs). However, growers can be reluctant to expose plants to drought stress because they do not want to negatively affect overall plant quality and marketability. Knowing how and when stem elongation is affected by water availability will help to increase our understanding of how elongation can be controlled without reducing plant quality. Rooted *Hibiscus acetosella* Welw. ex Hiern. cuttings were grown in a growth chamber set to a 12-hour photoperiod at 25 °C. Two plants of similar size were used for each replication of the study to compare growth under well-watered and drought-stressed conditions. Time lapse photography was used to determine the diurnal patterns of elongation over the course of the replications. Evapotranspiration was measured using load cells. Well-watered and drought-stressed plants had similar diurnal patterns of elongation and evapotranspiration, demonstrating that both follow circadian rhythms and are not just responding to environmental conditions. Stem elongation was greatest at night and coincided with evapotranspiration decreases, with greatest elongation shortly after the onset of darkness. Elongation was minimal between 800 and 1000 HR when evapotranspiration increases. During the drought-stress portion of the replications, elongation of drought-stressed plants was 44% less than well-watered plants. Final plant height and shoot dry weight for the drought-stressed plants were 21% and 30% less than well-watered plants, respectively. Total leaf area, number of leaves, and number of new visible internodes were greater for well-watered plants than drought-stressed plants. Average length of visible internodes and leaf size were similar for drought-stressed and well-watered plants. If growers want to use drought stress for elongation control, they should ensure that plants are drought stressed before the onset of and during the dark period, when most elongation occurs.**

Controlling plant stem elongation is common in ornamental plant production. Height control is necessary to meet industry standards for target plant height (Fisher and Heins, 1995), to increase plant aesthetics by producing more compact plants (van Iersel and Nemali, 2004) and because compact plants are less expensive to ship (Burnett and van Iersel, 2008). Plant growth regulators are commonly used (Berghage and Heins, 1991; Currey and Lopez, 2011), but are not always desirable as there is growing concern about the use of agrochemicals in production and their presence in runoff (Kaufmann et al., 2000). The selection of cultivars with shorter internodes and smaller growth habits can be used to produce smaller plants (Ecke et al., 2004), but such cultivars are not available for many taxa.

Environmental conditions can also be altered to manipulate plant growth and subsequent height, including alteration of day and night temperatures (Kaufmann et al., 2000), changing the daily light integral, and adjusting plant spacing (Liu and Heins, 2002). Alteration of temperature and light conditions is not always possible depending on what other crops are growing in the greenhouse or when plants are grown outdoors. Plant spacing may not be able to be increased if there is not enough space available and can increase overall production costs. Deficit irrigation or drought stress can also limit elongation; however, many growers are reluctant to expose their plants to drought stress because they do not want it to negatively affect overall plant quality (Bailey and Whipker, 1998). Sensor-controlled irrigation has been used to precisely control the timing, severity, and duration of drought stress to control elongation of poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) (Alem et al., 2015). Alem et al. (2015) controlled the height of poinsettia with deficit irrigation by lowering substrate water content to 0.20 $m^3 \cdot m^{-3}$ until plant height was within the desired range to produce a target final height after which substrate water content was increased to 0.40 $m^3 \cdot m^{-3}$. This effectively lowered plant height without negatively impacting plant quality. With the development of wireless sensor networks for irrigation control in commercial greenhouses and nurseries, this technology will be available soon to growers (Kohanbash et al., 2013; Lea-Cox et al., 2013).

Diurnal patterns of elongation have been examined in many plant taxa. Circadian rhythms interact with environmental conditions to determine elongation rates. Stomatal conductance and transpiration are also controlled partly by the plant circadian clock (Farré, 2012). Stem elongation has diurnal patterns (Nozue and Maloof, 2006) and leaf growth is maximal during the day or night, depending on the taxa. Environmental factors can influence the rate of growth, but not the diurnal pattern (Ruts et al., 2012).

Knowing how and when stem elongation is affected by water availability will increase our understanding of how elongation can be controlled through drought stress without reducing plant quality. Our first objective was to quantify diurnal patterns of elongation of *H. acetosella* in response to well-watered and drought-stressed conditions. *H. acetosella* is a fast-growing herbaceous species with clear growth responses to irrigation volume and substrate water content (Bayer et al., 2013). Understanding the time of day when elongation occurs can be useful in using drought stress as a means of plant elongation control. Our second objective was to quantify the effect of rewatering on the elongation rate of previously drought-stressed plants. The results of this study can be used to determine the optimal time for applying drought stress for elongation control.

Materials and Methods

Plant material. Research was conducted in a growth chamber at the University of Georgia in Athens, GA, from 17 Feb. to 1 June 2014. Six individual replications, with one well-watered and one drought-stressed plant each, lasted 11 to 19 d. *H. acetosella* 'Panama Red' (PP20121) terminal cuttings taken from one stock plant or clones of the stock plant were rooted in a peat-perlite substrate (Fafard 1P; Fafard Inc., Agawam, MA) for 5 to 10 d after which the rooted cuttings were transplanted into 2.4-L containers filled with a peat-perlite substrate (Fafard 1P, Fafard, Inc.). Cuttings were rooted every 10 to 14 d to have similar size

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plants for each individual replication. Plants were grown in a growth chamber (E-15; Conviron, Winnipeg, Manitoba, Canada) set to a 12-h photoperiod (0800 to 2000 HR) and a constant temperature of 25 °C, similar to the conditions during data collection. Plants were given 5–7 d for root establishment before onset of a replication. Fertilizer was supplied with a nutrient solution (Peters 15–5–15 Cal-Mag; Scotts, Marysville, OH; 15N–2.2P–12.45K) at a rate of 100 mg·L^{-1} nitrogen as needed.

Treatments and data collection. Two plants similar in size were chosen for each of the six replications of the study. Axillary branches were removed so that only the central shoot remained. For the first three replications, plants were kept well watered for the first 3 to 4 d of the replication, after which one plant remained well watered while the other was allowed to become drought stressed over the remaining 6 to 11 d, only watering with ≈200 to 400 mL after wilting occurred. This provided enough water to keep the plants alive, but not to fully rehydrate them. For the next three replications, plants were kept well watered for the first 3 to 6 d after which one plant remained well watered and the other was allowed to become drought stressed by completely withholding water over the next 6 to 8 d after which it was again returned to well-watered conditions for an additional 2 to 7 d to determine if nodes with reduced elongation stayed short or whether non-stressed elongation resumed on rewatering. The total duration of the six replications differed because of differences in elongation rate among replications. Data collection was concluded when the plants grew out of the field of view of the camera.

Well-watered plants were hand watered daily to above a weight of ≈1.5 kg (pot with substrate + plant), which was the weight of the well-watered plants at the start of the replication. The decrease in weight (pot with substrate + plant) of drought-stressed plants from well-watered to wilting conditions was between 0.71 and 0.96 kg, which is a decrease in volumetric water content of ≈0.36 to 0.48 m^3·m^{-3}. Before the start of each replication, plant height, number of internodes, internode lengths, stem diameter, and number of leaves were measured.

The weight of each plant was measured using individually calibrated load cells (LSP-10; Transducer Techniques, Temecula, CA) mounted on steel platforms with an acrylic platform on top of each load cell. Plant mass was measured every minute and averages were recorded by the data logger (CR1000; Campbell Scientific, Logan, UT) every 10 min. Hourly evapotranspiration was determined as the decrease in pot weight in 1 h after correcting for irrigation when needed. Environmental conditions were measured using a temperature and relative humidity sensor (HMP50; Vaisala, San Jose, CA) and a quantum sensor (SQ-110; Apogee Instruments, Logan, UT) with measurements averaged and recorded every 10 min.

Daytime temperature in the growth chamber averaged 25.5 °C ± 0.021 and night temperature averaged 24.4 °C ± 0.018. Relative humidity fluctuated both over the course of an individual replication and among replications ranging between 14% and 65%. Vapor pressure deficit also varied over the course of an individual replication and among replications, ranging between 1.1 and 2.8 kPa. Average photosynthetic photon flux density, measured at container height, was 324 μmol·m^{-2}·s^{-1}.

Time lapse photography (Pentax WG-1; RICOH Imaging Company, Denver, CO) was used to take hourly pictures of both plants and a meter stick in the same image. Hourly stem elongation was measured using image analysis software (Image J; U.S. National Institutes of Health; Bethesda, MD). Hourly elongation is the increase in height at the stated hour compared with height at the previous hour (i.e., stem elongation at 2000 HR is the elongation between 1900 and 2000 HR).

At the conclusion of each replication, height, number of internodes, internode lengths, stem diameter, and number of leaves were recorded. Shoots were cut off at the substrate surface and were dried at 80 °C after which dry weight was determined. Compactness was calculated as shoot dry weight/shoot length. Leaf area was measured using a leaf area meter (LI-3100; LI-COR, Lincoln, NE) and used to determine total leaf area per plants as well as the average size of all leaves on a plant.

Experimental design and data analysis. The experiment was designed as a randomized complete block with six replications and two plants per replication (one well watered and one drought stressed; $n = 6$). Experimental units were individual plants. Data were analyzed using the PROC TTEST and PROC MIXED procedures of SAS (SAS Version 9.2; SAS Institute, Cary, NC), with $P \leq 0.05$ considered to be significant. Treatment means were separated using the PDIFF option of PROC MIXED. Regression analysis was done using proc GLM (SAS 9.3; SAS, Cary, NC).

Results and Discussion

Total height increase was 30% less for the drought-stressed than the well-watered plants ($P = 0.0077$) over the course of the 11 to 19 d replications (Table 1). During the drought-stressed period of the replications, elongation of drought-stressed plants was 44% less than that of the well-watered plants (Fig. 1). Final height of plants that were rewatered was 21% less than well-watered plants (data not shown). Elongation rate varied by replication (data not shown); likely because of fluctuations in environmental conditions between replications and natural variations in growth. The final number of new visible internodes was higher for well-watered plants than drought-stressed plants ($P = 0.054$; Table 1). Drought-stressed and then rewatered plants had 15% fewer new internodes and drought-stressed only plants had 37% fewer new internodes than well-watered plants (data not shown). Average length of all visible internodes was similar among treatments ($P = 0.51$; Table 1). We hypothesize that the difference in the number of new visible internodes between well watered and drought stressed is due to unelongated, nonvisible internodes near the growing point of the drought-stressed plants. Development and differentiation in the apex is largely temperature driven (Atkinson and Porter, 1996), while elongation is water dependent (Hsiao and Xu, 2000); this would mean that new internodes could develop, while drought stress would inhibit elongation of those internodes. Shoot dry weight was 30% less for the drought-stressed than the well-watered plants ($P = 0.037$; Table 1).

Drought stress has been used to reduce elongation in many species including *Gaura lindheimeri* Engelm. & Gray 'Siskiyou Pink' (Burnett and van Iersel, 2008), *Rhododendron* 'Catawbiense Boursault' and *Rhododendron* 'Old Port' (Koniarski and Matysiak, 2013), *Tagetes erecta* L. 'Queen Sophia' (van Iersel and Nemali, 2004), *Salvia splendens* F. Sellow. Ex Roem. & Shult. 'Bonfire' (Burnett et al., 2005), and *H. acetosella* 'Panama Red' (Bayer et al., 2013). Stem elongation is reduced by drought stress due to reduced cell division and expansion (Hsiao and Xu, 2000), which could explain the lower number of visible internodes under drought stress. *G. lindheimeri*, *T. erecta*, and *H. acetosella* were smaller, but not more compact, with drought stress. Compactness, shoot dry weight per unit shoot length, is a measure of plant density and an indicator of quality (van Iersel and Nemali, 2004). Compactness of well-watered and drought-stressed plants was not different in this study (Table 1); however, well-watered plants formed more axillary shoots than drought-stressed ones ($P = 0.011$; data not shown).

Leaf area and number of leaves were ≈36% lower for drought-stressed than for well-watered plants ($P = 0.012$ and $P = 0.016$, respectively; Table 1), but the average leaf size was unaffected by drought (Table 1). Reduced leaf area with drought stress has been reported for *G. lindheimeri* (Burnett and van Iersel, 2008), *Rhododendron* 'Catawbiense Boursault' and *Rhododendron* 'Old Port' (Koniarski and Matysiak, 2013), *S. splendens* (Burnett et al., 2005), and *T. erecta* (van Iersel and Nemali, 2004). Leaf size of *H. acetosella* 'Panama Red' was reduced with decreasing substrate volumetric water content (Bayer et al., 2013). Reduced leaf area of *T. erecta* under drought was the result of fewer leaves and reduced leaf size (van Iersel and Nemali, 2004). Leaf area is reduced with drought stress due to reduced cell elongation with low soil water potential (Hsiao and Xu, 2000; Lambers et al., 2008). The lack of difference in average leaf size in this study was unexpected as leaf size is normally reduced with drought stress. Since well-watered plants branched more than drought-stressed ones, they may likely also have

Table 1. Growth measurements for well-watered and drought-stressed *Hibiscus acetosella* 'Panama Red'. Increase in height is over the course of the 7 to 11 d drought-stress period. Other measurements are over the course of the 11–19 d replications including the rewatering of stressed plants. Compactness was calculated as shoot dry weight/shoot length (n = 6).

Treatment	Ht increase (mm)	Shoot dry wt (g)	Compactness ($g \cdot m^{-1}$)	Avg internode length (mm)	Number of new visible internodes	Leaf area (cm^2)	Number of leaves	Avg leaf size (cm^2)
Well watered	285	6.5	8.6	34.7	10	1,291	101	12.8
Drought stressed	171	4.5	7.3	33.4	8	808	66	12.3
P value	0.0077	0.037	0.19	0.51	0.054	0.012	0.016	0.65

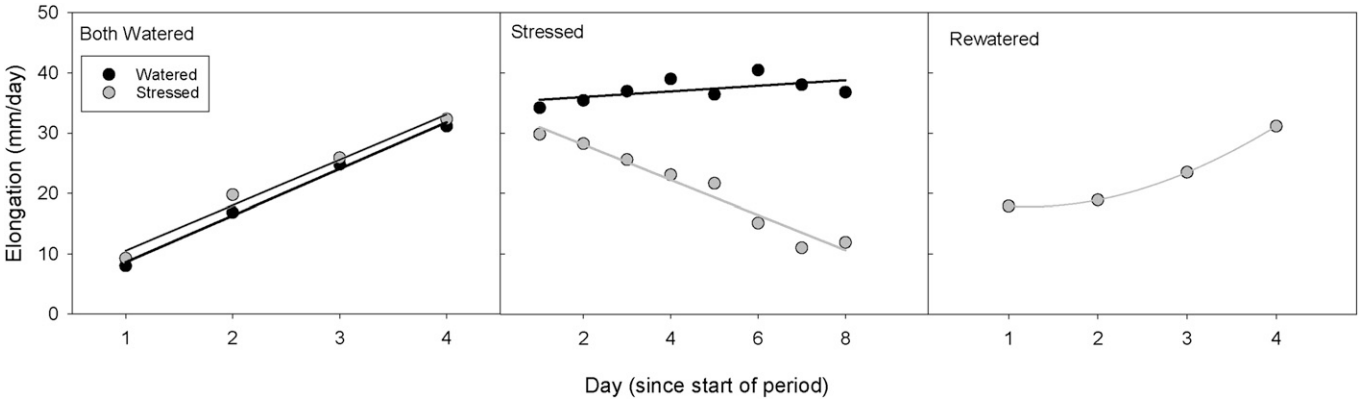

Fig. 1. Daily elongation of *Hibiscus acetosella* 'Panama Red' over the course of the 11–19 d replications. Graphs have been separated into periods that both plants were watered (left), watered or stressed (middle), and after rewatering of stressed plants (right) to show changes in daily elongation during the different periods. Daily elongation was not different for the plants when both were well watered. After the onset of drought stress, daily elongation rate was greater for well-watered plants than stressed plants ($P < 0.0001$; Fig. 1) with the reduction in elongation due to drought stress increasing with days after onset of drought stress. Elongation of previously drought-stressed plants increased gradually during the 4 d after rewatering.

produced more new leaves. If these new leaves did not fully expand by the end of a trial, the relatively small size of these expanding leaves may have biased the average leaf size of well-watered plants. The increase in stem diameter was similar for drought-stressed and well-watered plants (data not shown).

Daily elongation rate was similar for plants in both treatments during the first 4 d of a replication when both plants were well watered (Fig. 1). After the onset of drought stress, daily elongation rate was higher for well-watered plants than stressed plants ($P < 0.0001$; Fig. 1) with the reduction in elongation due to drought stress increasing with time after the onset of drought stress ($P = 0.019$; Fig. 1). Daily elongation during the drought-stress period averaged 39.4 ± 1.7 and 20.9 ± 1.8 mm for well-watered and drought-stressed plants, respectively. Under well-watered conditions, plant height increased by ≈6% per day. Daily elongation rate for drought-stressed plants was 13% less than well-watered plants within 2 d of the onset of drought stress and was 33% less at the end of the drought-stress period.

Elongation rate of well-watered plants was higher than that of the stressed plants at any time of the day ($P < 0.0001$) within 2 d of the onset of the drought stress, with both well-watered and drought-stressed plants exhibiting similar diurnal patterns of elongation (Fig. 2). The daytime elongation rate averaged 1.05 ± 0.21 and 0.31 ± 0.041 mm/h and nighttime elongation 2.41 ± 0.20 and 1.57 ± 0.12 mm/h for well-watered plants and drought-stressed plants, respectively. Elongation rate was lowest between 0800 and 1000 HR at 0.44 and 0.12 mm/h and highest around 2000 HR with elongation rates of 3.53 and 2.87 mm/h for well-watered plants and drought-stressed plants, respectively. Elongation rate was relatively steady from 1000 to 1900 HR and from 2100 to 0700 HR.

Circadian and diurnal rhythms of stem elongation rates have been reported (Nozue and Maloof, 2006) for plants grown under constant temperature and light as well as light and dark cycles (Dowson-Day and Millar, 1999; Lecharny and Wagner, 1984). Inflorescence stem elongation of *Arabidopsis thaliana* L. (Jouve et al., 1998) and stem elongation of *Chenopodium rubrum* (Lecharny and Wagner, 1984) have circadian rhythms even in constant light. Dowson-Day and Millar (1999) reported a diurnal pattern with maximum hypocotyl elongation rates of *A. thaliana* at dusk with reductions in elongation rate at dawn. This is similar to our results with maximum elongation around 2000 HR with a burst of elongation occurring soon after the start of darkness and minimal elongation between 0800 and 1000 HR, the start of the light period. Conversely, Neily et al. (1997) reported stem elongation rate of snapdragon declined at night and increased during the day. Patterns of stem elongation rate of zinnia changed with developmental stage, with elongation rate greatest early in the day during early development and at night as plants matured (Neily et al., 1997). This suggests that stem elongation patterns are species and developmentally dependent. Similarly, leaf elongation rates have been reported to show growth patterns with maximum elongation occurring around dawn or at night depending on species (Ruts et al., 2012).

There was an inverse relationship between elongation and evapotranspiration rate, with evapotranspiration high during the day and low at night and elongation greatest at night (Fig. 2). This suggests that elongation is highest at night due to rehydration when stomata close at night and increasing turgor pressure of the plant, allowing for cell elongation. Sufficient turgor pressure is needed to plastically stretch the cell well allowing for cell expansion (Boyer and Silk, 2004; Passioura and Boyer, 2003). Evapotranspiration was low when the lights were off, increasing rapidly between 0800 and 0900 HR after the lights were turned on and rapidly decreasing between 2000 and 2100 HR after the lights were turned off, indicative of stomatal opening in response to light. Elongation was highest between 2000 and 2100 HR and was 59% and 82% higher at night than during the day for the well-watered and drought-stressed plants, respectively. Elongation rate began to decrease at around 0700 HR (before the start of the light period), suggesting that elongation is responding to a circadian pattern rather than just a response to light. Lower transpiration rates at night could mean that more water is available for cell expansion and elongation, rather than transpiration, which could explain greater nighttime elongation. A comparison of daily evapotranspiration and elongation shows the reduction in elongation rate due to drought stress ($P = 0.01$). Rewatering drought-stressed plants rapidly increased evapotranspiration ($P < 0.0001$; Fig. 3); however, elongation rate remained restricted and gradually increased from 18 to 30 $mm \cdot d^{-1}$ during the 4 d after rewatering (Fig. 1). This suggests that drought

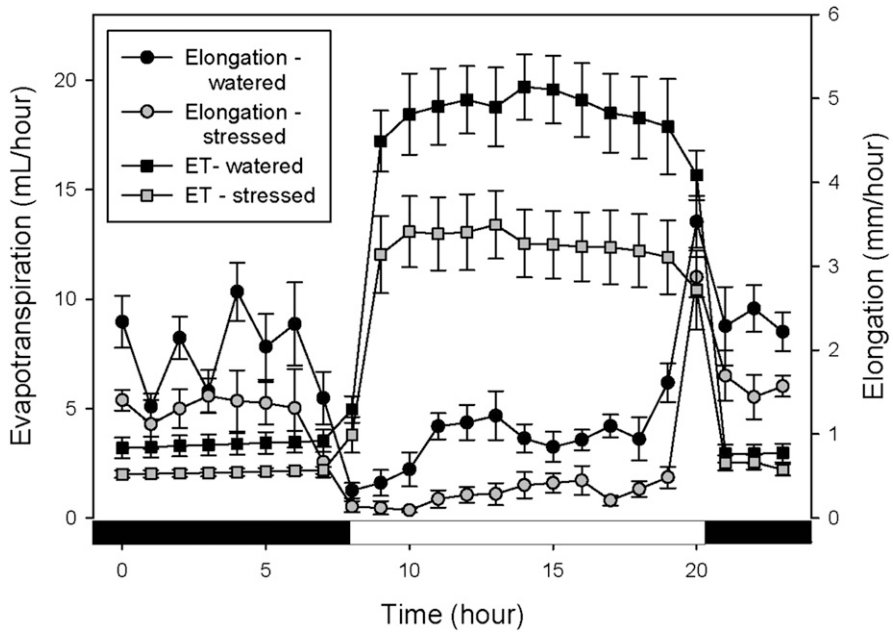

Fig. 2. Hourly evapotranspiration (ET, squares) and elongation (circles) of *Hibiscus acetosella* 'Panama Red' over the course of 24 h for the 11–19 d replications. Data for drought-stressed plants begins 1 d after the onset of drought. A diurnal pattern of ET can be seen with increased ET when the lights are turned on (0800 HR) and decreased when the lights are turned off (2000 HR). Elongation also exhibits a diurnal pattern with reduced elongation during the day and increased elongation at night. For both ET and elongation, well-watered and drought-stressed plants follow similar diurnal patterns with drought-stressed plants having reduced ET and elongation. Elongation and ET data at a specific time indicate the elongation and ET during the previous hour. Black and white boxes at the bottom of the graph indicate darkness and light, respectively. Error bars indicate standard errors.

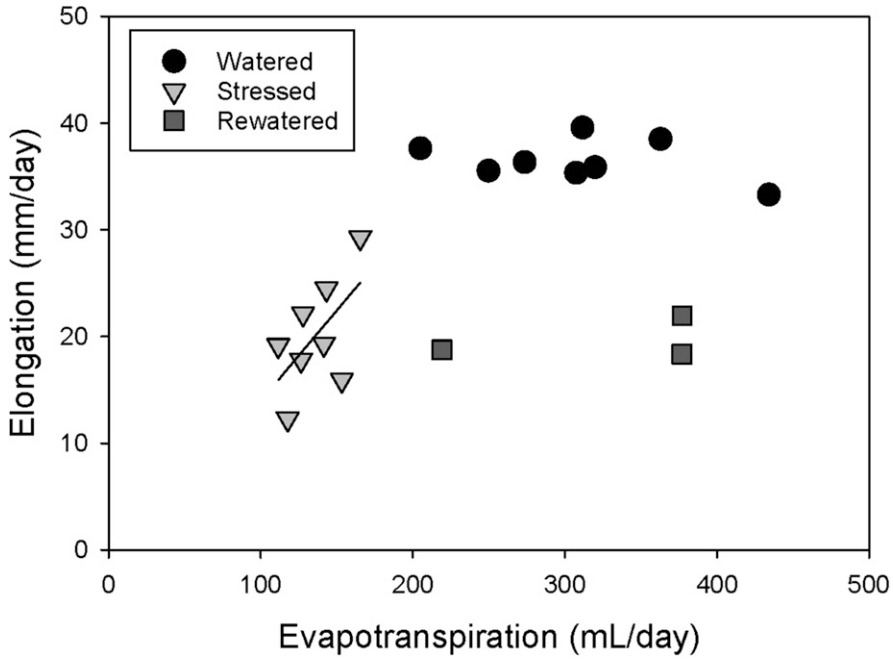

Fig. 3. Daily elongation of well-watered (black circles), drought-stressed (light gray triangles), and stressed then rewatered (dark gray squares) *Hibiscus acetosella* 'Panama Red' as a function of daily evapotranspiration. The relationship between evapotranspiration and elongation shows that as drought stress reduces evapotranspiration, the elongation rate is reduced as well ($P = 0.01$). Rewatering stressed plants resulted in increased evapotranspiration; however, elongation rate remained low.

causes temporary changes in cell wall plasticity that prevent rapid elongation after the drought stress has been relieved. Such a lasting effect of drought stress on elongation of leaves of dicots has been reported previously (Granier and Tardieu, 2009).

Evapotranspiration is influenced by environmental conditions including light, temperature, and vapor pressure deficit, but also by stomatal opening and closing, which is regulated partly by circadian mechanisms (Hotta et al., 2007). In well-watered *A. thaliana* plants, stomata close at midday, not in response to water status but due to circadian control of the guard cells (Dodd et al., 2005). Stomata also open in anticipation of dawn (Hotta et al., 2007) indicating circadian control. Evapotranspiration began to increase around 0700 HR and decrease around 1900 HR, an hour before lights were turned on and off, respectively. This could suggest stomatal opening and closing in anticipation of dawn and dusk. Diurnal changes in transpiration can be due to changes in abscisic acid (ABA) levels, which are influenced by the circadian clock (Tallman, 2004). Environmental influences can alter the intensity of the circadian responses (Hotta et al., 2007). Reduced leaf area surface of drought-stressed plants contributes to reduced transpiration (Obidiegwu et al., 2015; Patanè, 2011). The combination of increased ABA levels, reduced leaf area, and drought stress could explain reduced evapotranspiration in drought-stressed plants.

Conclusions

Both drought-stressed and well-watered plants followed a similar diurnal pattern of elongation, agreeing with previous research that elongation depends on a circadian rhythm and is not only a response to environmental conditions. Well-watered plants elongated 10 $mm \cdot d^{-1}$ more than drought-stressed plants. Daily elongation showed that as the severity of drought stress increased over the course of the study, the rate of elongation of the drought-stressed plants continued to decrease. Results of this study show that controlling stem elongation and growth of plants is possible with irrigation management. In this study, diurnal patterns show that elongation of *H. acetosella* is greatest at night, with greatest elongation following the onset of darkness when evapotranspiration decreased. Elongation is minimal between 0800 and 1000 HR when evapotranspiration increases. If growers want to use drought stress for elongation control, they should ensure that plants are drought stressed before the onset of and during the dark period, when most elongation occurs. It is also important to consider that the effects of drought stress on elongation can persist after the drought stress has been relieved.

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