Thermoperiodicity in Shoot Elongation of Purple Nutsedge

Wen-Hao Sun¹ and Roy K. Nishimoto²

Department of Horticulture, University of Hawaii, Honolulu, HI 96822-2279

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ABSTRACT. The effect of single and daily alternating temperature cycles on elongation of emerged buds of purple nutsedge (*Cyperus rotundus* L.) was characterized to determine whether shoot elongation responded to alternating temperature as a thermoperiodic function. Glasshouse-grown tubers with emerged buds of 2 to 5 mm in length were used in experiments. Shoot extension increased at 35 °C after 7 days, but no significant shoot extension occurred at all other constant temperatures of 20, 25, 30, 40, and 45 °C. However, 2- to 8-fold increases in shoot extension occurred at alternating temperatures of 25/15, 30/20, 35/25, 40/30, 41/35, 42/38, and 45/35 °C (12/12 hours) as compared to the respective mean constant temperatures. Daily temperature differences of 2 and 4 °C did not stimulate shoot elongation, while temperature differences of 8 and 12 °C caused an 8-fold shoot stimulation when compared to the 24 °C constant temperature. Shoot elongation increased with increasing numbers of alternating temperature cycles. The optimal duration of the lower and upper temperature phases differed depending on temperature regimes; at 40/30 °C, maximal elongation occurred with daily exposures of 40 °C for 1 to 3 hours and 30 °C for 23 to 21 hours respectively, while at 30/20 °C, maximal elongation occurred with daily exposures of 30 °C for 15 hours and 20 °C for 9 hours. These results suggest that elongation of purple nutsedge tuber buds responds to alternating temperature as a thermoperiodic function.

Sprouting of single tubers of purple nutsedge is thermally regulated (Holt and Orcutt, 1996; Miles 1991; Miles et al., 1996; Tripathi 1967; Ueki 1969). Miles et al. (1996) studied the effect of alternating temperatures on purple nutsedge tuber sprouting and showed that all tubers sprouted under alternating temperatures (35/25 °C, 12/12 h), while only 66% sprouted within 4 weeks at the constant mean temperature (30 °C). They defined sprouting as budbreak and shoot elongation to ≥ 10 mm.

Purple nutsedge tuber sprouting probably involves two steps: budbreak and elongation of the emerged bud (Nishimoto et al., 1995). Budbreak occurred within 2 weeks for $\approx 75\%$ of the tubers at constant 20 °C, or at relatively constant temperatures of ≈ 23 °C in the laboratory, but only $\approx 10\%$ of the emerged buds elongated > 10 mm (Nishimoto et al., 1995). Nearly all of the remaining dormant tubers were induced to the budbreak stage by a single 30-min 35 °C pulse (Sun and Nishimoto, 1997). Thus, the budbreak process occurs readily and can be triggered by high temperature. However, there is no information on thermal regulation of bud elongation of purple nutsedge. This research focused on the response of the elongation of the emerged bud to alternating temperatures and whether the response is thermoperiodic.

Thermoperiodicity or thermoperiodism refer to a physiological response of an organism to the alternation of high and low temperatures. The term thermoperiodicity in plants was coined by Went (1944). Went (1944) and other researchers (Dale, 1964; Friend and Helson, 1976; Wellensiek, 1957) indicated that the thermoperiodic effect could stimulate plant growth and development; their definition assumed that light and associated growth was important during part of the daily cycle. The thermoperiodicity concept provides a framework for characterizing the elongation response of purple nutsedge buds.

Thermoperiodicity is the plant response to alternating temperature rather than to different absolute temperatures. It is difficult to separate effects of alternating temperature from effects of the different temperatures themselves. The use of constant upper, lower (Went, 1944), or mean temperature of the alternation cycle (Haroon et al., 1972; Lionakis and Schwabe, 1984; Wellensiek, 1957) as a reference temperature is not sufficient to demonstrate thermoperiodicity because the growth response to constant temperature is not linear over a wide temperature range. The choice of suboptimal or supraoptimal temperatures for experiments can cause inconsistent effects over a wide temperature range (Friend and Helson, 1976). Thus, Dale (1964) and Friend and Helson (1976) tested for thermoperiodicity by assessing growth (dry weight, stem elongation, etc.) at the constant temperature where optimal growth occurred and compared that with growth at the alternating temperature regime with the same diurnal mean.

Thermoperiodism is not a phenomenon common to all species. Using Dale's definition of thermoperiodism, no evidence was found for a thermoperiodic response in dry weight of bean (*Phaseolus vulgaris* L.), cucumber (*Cucumis sativus* L.), maize (*Zea mays* L.), oat (*Avena sativa* L.), pea (*Pisum sativum* L.), tomato (*Lycopersicon esculentum* Mill) and wheat (*Triticum aestivum* L.) (Dale, 1964; Friend and Helson, 1976). A number of studies showed that growth of sugar cane (*Saccharum officinarum* L. hybrid 'Pintar') (Glasziou et al., 1965), sugar beet (*Beta vulgaris* L.) (Ulrich, 1952), tobacco (*Nicotiana tabacum* L.) (Haroon et al., 1972), soybean (*Glycine max* (L.) Merr) (Warrington et al., 1977), and cotton (*Gossypium hirsutum* L.) (Rajan and Blackman, 1975) under diurnally alternating temperature conditions was not greater than under constant temperature conditions with the same diurnal mean; these results indicate that there could be no thermoperiodicity in those plants when using growth parameters. However, the stimulation of germination by alternating temperature that occurs in numerous seeds (Benech Arnold et al., 1988; Harrington, 1923; Morinaga, 1926; Nishimoto and McCarty, 1997; Thompson et al., 1977; Totterdell and Roberts, 1980) would be expected to be classified as thermoperiodic if the proper alternating and constant temperature comparisons were made.

These experiments were designed to determine if shoot elongation responded to alternating temperature as a thermoperiodic

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¹Former graduate research assistant. Currently postdoctoral research associate, Department of Plant Molecular Physiology, University of Hawaii.

²Professor, to whom reprint requests should be addressed.

function, using Dale's (1964) criterion to test for thermoperiodicity. The shoot elongation response to attributes of the alternating temperature function such as the magnitude of the daily alternating temperature, the number of alternating cycles, and variations in the duration of lower and upper temperature was characterized.

Materials and Methods

TUBER SELECTION AND GROWTH CONDITIONS. Purple nutsedge tubers were obtained from glasshouse-grown plants and incubated at 20 °C for at least one week as described by Sun and Nishimoto (1997). After further incubation at prescribed temperature conditions for these experiments, tubers that had at least one sprout 2 to 5 mm in length were subjected to temperature treatments. Sprouted tubers were incubated on two layers of filter paper moistened with 3.5 ml deionized water in a 100 × 15 mm petri dish enclosed in a polyethylene bag to conserve moisture. The relative humidity in the incubator was maintained at 60% to 70%.

TEMPERATURE TREATMENTS. Programmable incubators (± 1.0 °C) were used for the daily alternating temperature regimes with equal duration (12 h) of upper and lower temperature. The shorter periods of alternating temperatures were provided by transferring tubers between incubators at designated temperatures for the required time intervals. It took ≈ 30 min for the tuber's surface temperature to change from 20 to 35 °C or vice versa, and this time was included in the reported heating times.

THERMOPERIODIC EFFECT. Tubers with budbreak were incubated at constant 25 °C for 7 d before use in this experiment. The optimal constant temperature for shoot elongation was determined by comparing shoot elongation under six constant temperatures ranging from 20 to 45 °C at intervals of 5 °C. The alternating temperature regimes of 25/15, 30/20, 35/25, and 40/30 °C at 12 h for each temperature were compared to the constant temperature regimes to assess for thermoperiodicity of shoot elongation.

An experiment was also conducted to determine the elongation response at constant and mean alternating temperatures above the optimum of 35 °C. The treatments included constant temperatures of 38, 40, and 42 °C, and alternating temperature regimes of 41/35 °C; 42/38 °C; 45/39 °C; and 45/35 °C, all at 12 h for each temperature. Tubers were held at constant temperatures of 25 °C for 7 d before initiation of the treatments.

MAGNITUDE OF DAILY ALTERNATING TEMPERATURES. Tubers with budbreak were incubated at constant 24 °C for 7 d before treatments of 24/24, 25/23, 26/22, 28/20, and 30/18 °C for another 7 d; daily temperature differences were 0, 2, 4, 8, and 12 °C, respectively. The duration of the high and low temperature phases was 12 h each.

NUMBER OF ALTERNATING TEMPERATURE CYCLES. Tubers were incubated at constant 20 °C for 7 d before treatments of one, three, five and seven daily alternating temperature cycles of 40/20 °C (1/23 h). After the specified number of daily alternating temperature cycles, tubers were maintained at constant 20 °C. The effect of cumulative heat of each high temperature pulse on shoot elongation was assumed to be negligible due to the short period of high temperature.

DURATION OF UPPER AND LOWER TEMPERATURE PHASES. Tubers with budbreak were incubated at 25 °C for 7 d before treatments. Two alternating temperature regimes (30/20 °C and 40/30 °C) with different exposure times at the upper and lower temperature regimes were imposed for 7 d. The upper and lower phase temperatures were 0/24 h, 1/23 h, 3/21 h, 6/18 h, 9/15 h, 12/12 h, 15/9 h, 18/6 h, 21/3 h, 23/1 h, and 24/0 h, respectively.

SHOOT LENGTH MEASUREMENTS. The shoot length from the bud base to the tip of the scale leaf or primary leaf was measured after

7 d. If one tuber possessed several shoots, the longest shoot was reported. Miles et al (1996) recorded a tuber as sprouted if a shoot exceeded 10 mm, and, to provide a basis for comparison, the number of shoots longer than 10 mm was also recorded.

STATISTICAL ANALYSIS. Each experiment was conducted as a completely randomized design, consisting of four replicate dishes per treatment with 10 tubers per dish. All experiments were conducted at least twice, but some repeat experiments had slightly different temperature regimes. Results between experiments were similar, and data from one of the experiments are shown. Data were subjected to analysis of variance (ANOVA) to determine sources of variation and provide the estimates for calculating the standard errors of means. The sprouting response to the number of daily alternating temperature cycles was analyzed by nonlinear regression. Duncan's multiple range test was used to determine whether treatments were significantly different.

Results

THERMOPERIODIC EFFECT. The optimal constant temperature for shoot elongation of purple nutsedge was 35 °C, where shoot length was 16 mm after 7 d incubation (Fig. 1). At constant temperature of 20, 25, 30, 40, and 45 °C, shoot length was only 1 to 6 mm, and the means were not different from each other (Fig. 1). At 45 °C, no growth occurred and most shoots were necrotic.

Shoot elongation at all alternating temperature regimes was greater than at the respective constant temperature regimes (Fig. 1). The longest shoot length (58 mm) occurred at the alternating temperature regime of 35/25 °C, and was >8-fold greater than at the 30 °C constant temperature (Fig. 1). Shoot elongation was >2-fold greater at the alternating temperature regime of 40/30 °C (12/12 h), than at the 35 °C optimal constant temperature (Fig. 1); at 40/30 °C (12/12 h), 98% of the shoots were longer than 10 mm (data not shown).

Thermoperiodicity was further tested by examining the extent of elongation caused by alternating and constant temperatures greater than the optimum temperature (Table 1). At mean temperatures exceeding the optimal constant temperature (35 °C), alternating temperature regimes generally caused more elongation than at the corresponding mean constant temperatures, including one

Fig. 1. Response of purple nutsedge shoot elongation to constant and alternating temperature regimes. The response of shoot elongation to constant temperatures is depicted by the line graph, and the alternating temperature regimes by the bar graph. Data points within alternating temperatures or within constant temperatures with different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

Table 1. Response of purple nutsedge shoot elongation to supraoptimal constant temperatures and alternating temperature regimes.

Temp regime (°C)	Shoot length (mm)
38	9.1 c ^z
41/35 (12/12 h)	27.7 a
40	9.3 c
45/35 (12/12 h)	16.1 b
42/38 (12/12 h)	15.3 b
42	3.1 c
45/39 (12/12 h)	5.5 c

^zMeans followed by different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

regime with only a 4 °C daily temperature difference. The only exception was for the highest alternating temperature regime tested (45/39 °C), where elongation was not different than in the 42 °C constant temperature regime (Table 1).

MAGNITUDE OF DAILY ALTERNATING TEMPERATURES. Shoot length at alternating temperatures with daily temperature differences of 8 or 12 °C increased to >8-fold compared to the constant mean temperature of 24 °C, and 88% and 98% of the shoots were longer than 10 mm, respectively (Fig. 2). Exposure to daily temperature differences of 2 or 4 °C around a 24 °C mean temperature did not significantly promote shoot extension within 7 d, and only 28% of the shoots subjected to a difference of 4 °C were longer than 10 mm.

NUMBER OF FLUCTUATING TEMPERATURE CYCLES. Shoot elongation increased in a sigmoidal fashion with increasing alternating temperature cycles (Fig. 3). A sigmoidal curve accounted for 97% of the variation in shoot elongation.

DURATION OF UPPER AND LOWER TEMPERATURE PHASES. The effective duration of the high and low temperature periods varied with different temperature regimes. Maximal shoot length occurred with upward shifts from 30 to 40 °C for 1 to 3 h and shoot length declined as the daily duration of the 40 °C upper temperature exceeded 3 h (Fig. 4). In the 30/20 °C fluctuating temperature regime, shoot length was <50% of maximum with a 1 to 3 h upward shift from 20 to 30 °C and was maximum at ≈15 h at 30 °C (Fig. 4). Shoot length declined as the duration of the upper temperature (30 °C) increased from 15 to 24 h.

Discussion

Greater elongation at alternating daily temperatures than at the mean constant suboptimal, optimal, and supraoptimal temperatures over a wide range of constant temperatures (Fig. 1, Table 1) shows that the purple nutsedge shoot elongation response was thermoperiodic. The shoot elongation response met the established criteria for thermoperiodicity, which is the demonstration of greater growth at alternating temperature than at the optimal constant mean temperature (Dale, 1964; Friend and Helson, 1976).

Diurnally alternating temperatures caused more shoot elongation than constant temperatures with the same mean temperature on a wide range of species. These species included Easter lily (*Lilium longiflorum* Thunb.) (Erwin et al., 1989), chrysanthemum (*Chrysanthemum morifolium* Ramat.) (Karlsson and Heins, 1986), bellflower (*Campanula isophylla* Mor.) (Moe, 1990), cucumber (Grimstad and Frimanslund, 1993), soybean (Warrington et al., 1977), and tomato (Heuvelink, 1989). Those studies did not test for thermoperiodicity at optimal constant temperatures as suggested by Dale (1964), although the stimulation of shoot elongation by

diurnally alternating temperature appeared to be a relatively common phenomenon.

Few studies have pursued an understanding of the alternating temperature stimulation of shoot elongation. The stimulation of shoot elongation by alternating temperature only occurred when the high temperature was associated with the day period; if the low temperature was associated with the day period, shoot elongation was equivalent or lower than at constant temperature (Erwin et al., 1989; Grimstad and Frimanslund, 1993; Jensen et al., 1996; Moe, 1990). Erwin et al. (1989) stated that their unpublished studies showed that the effect of temperature on Easter lily shoot elongation was not affected by increasing or decreasing the irradiance under which plants were grown between 50 and 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Moe (1990) also reported that the thermomorphogenic effect on shoot elongation of bellflower was not greatly influenced by changes in irradiance levels. Thus, both Erwin et al. (1989) and

Fig. 2. Response of purple nutsedge shoot elongation to the daily temperature difference of the alternating temperature cycle. Each alternating temperature regime has 12 h high and 12 h low temperature around a mean temperature of 24 °C. Bars within a response variable (length or percent) with different letters differ significantly by Duncan's multiple range test, $P = 0.05$. The mean separation of shoot length and the number of shoots larger than 10 mm are identical, so the bar and line graphs share the same letters.

Fig. 3. Response of purple nutsedge shoot elongation to the number of alternating cycles. One high temperature pulse (40 °C for 1 h) was inserted after 23 h incubation at 20 °C in each alternating cycle. Tuber sprouts were incubated at 20 °C after exposure to the indicated number of alternating cycle(s). The fitted model is $Y = -0.5913 + 23.8404 / (1 + \exp(-(x + 1.4233) / 1.6189))^{6.2}$. Observations with the same value are hidden from view.

Fig. 4. Response of purple nutsedge shoot elongation to the duration of upper and lower temperature phases of the alternating temperature regimes (30/20 and 40/30 °C). After seven cycles, the shoot length was determined. The values for shoot elongation at constant lower and higher temperatures are at 0 and 24 h respectively. Horizontal bars represent $\pm$ SE.

Moe (1990) suggested that thermomorphogenesis was probably not related to irradiance levels and carbohydrate supply, and that it may be mediated by differences in gibberellin (2,4 α ,7-trihydroxy-1-methyl-8-methylenegibb-3-ene-1,10-dicarboxylic acid 1,4 α -lactone). Erwin et al (1989) showed that a gibberellin biosynthesis inhibitor, ancymidol ((α -cyclopropyl- α -(4-methoxyphenyl)-5-pyrimidinemethanol) reduced shoot elongation and its effect was decreased as the difference between day and night temperature decreased. Similar results were obtained with daminozide ((butanedioic acid mono(2,2-dimethylhydrazide) on bellflower, while applications of GA₃ overcame the stem elongation inhibition (Moe, 1990). In addition, Jensen et al. (1996) showed that diurnally alternating temperatures that stimulated shoot elongation in bellflower were accompanied by an increase in GA₁, GA₁₉, and GA₄₄.

The strong control of purple nutsedge shoot elongation by varying the duration of the high and low temperature periods with different temperature regimes has important practical implications. Alternating temperature cycles of only 1 h at 40 °C and 23 h at 30 °C treatment were sufficient to obtain a maximal level of shoot elongation, while shoot elongation declined as the duration at lower phase temperature decreased over the range from 18 to 0 h (Fig. 4). A similar pattern of shoot elongation was observed at the lower alternating temperature regime of 30/20 °C (Fig. 4). Thus, models to predict emergence of purple nutsedge should consider the daily fluctuation in temperature.

An increased understanding of temperature regulation of the sprouting process may be valuable for the imposition of management strategies. Purple nutsedge budbreak and shoot elongation are thermally regulated and require a daily temperature differential (Nishimoto et al., 1995). For budbreak, only the upward shift in a fluctuating temperature regime was effective; a single short-duration high temperature pulse was sufficient to terminate dormancy (Sun and Nishimoto, 1997). In contrast, shoot elongation was stimulated by both upward and downward shifts (Fig. 1, Table 1). Multiple daily alternating temperature cycles were required for maximal elongation, and increasing numbers of high temperature pulses stimulated shoot elongation in a sigmoidal pattern (Fig. 3).

Increasing the daily temperature difference increased tuber sprouting (shoots exceeded 10 mm) and shoot extension (Fig. 2). This agrees with the finding of Miles et al. (1996). Shoot extension was also greater when the daily temperature difference was 4 °C around a mean of 40 °C (Table 1) rather than 24 °C (Fig. 2). However, little shoot elongation occurred when the mean of the alternating temperature increased to 42 °C or at constant 42 °C (Table 1) and 45 °C (Fig. 1). This is consistent with previous studies, where no tuber sprouting occurred if tubers were exposed to constant temperatures of 43 to 45 °C (Holt and Orcutt, 1996; Miles, 1991; Ueki, 1969).

Both the mean temperature and the daily temperature difference are important factors in the application of soil solarization to increase sprouting of purple nutsedge (Miles, 1991). The mean daily soil temperature at 15 cm depth ranged from 22 to 27 °C at a low elevation site in Hawaii and the daily difference between minimum and maximum was <2 °C; $\approx$ 70% of the tubers sprouted within 3 to 5 weeks under these conditions (Miles, 1991). Under soil solarization, the mean daily soil temperature at 15 cm depth increased to 28 to 32 °C and the daily difference between minimum and maximum was $\approx$ 4 to 5 °C; under these conditions $\approx$ 97% of the tubers sprouted (Miles, 1991). Thus, soil solarization may be useful to stimulate and synchronize purple nutsedge emergence, which could be followed by application of an effective herbicide.

The requirement for multiple cycles of alternating temperature to cause elongation of purple nutsedge may be important to its survival. Budbreak occurs readily for most tubers without any alternating temperature stimulation, and dormant tubers may be readily released from dormancy by a brief high temperature pulse (Sun and Nishimoto, 1997). If the temperature remains relatively constant, most purple nutsedge buds will not elongate. The sprouts will emerge when the temperature is high enough with adequate temperature difference between day and night. Favorable alternating temperature conditions occur when a plant canopy above the soil surface is removed (Rubin and Benjamin, 1984). Under such conditions, purple nutsedge can grow without competition with other plants. This sensing mechanism would assess whether environmental conditions were favorable or adverse for purple nutsedge and thereby regulate its emergence.

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