Dormancy Release of Purple Nutsedge Tuber Buds by a Single Thermal Pulse

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 fluctuating temperature cycles on budbreak of purple nutsedge (*Cyperus rotundus* L.) tubers was characterized to determine whether the budbreak response was a trigger or rhythmic action. Glasshouse-grown tubers were incubated at 20 °C for 2 weeks, and the nonsprouted tubers were used in experiments. A single 30-minute temperature pulse from 20 to 35 °C caused 80% budbreak, while tubers without the thermal pulse had only 25% budbreak. Increasing the duration of the single 35 °C temperature pulse from 30 minutes to 12 hours did not increase budbreak. Even a 3-minute 35 °C pulse caused 63% budbreak. A single gradual shift (0.02 °C per minute) from 20 to 35 °C was as effective as a rapid shift (0.5 °C per minute) in stimulating budbreak. Nonsprouted tubers preincubated at 25 °C were stimulated to cause budbreak by exposure at 35 °C for 12 hours, but not at 15 °C for 12 hours. A single temperature pulse of at least 10 °C differential (from 20 to 30, 35, or 40 °C) stimulated budbreak, while a 5 °C differential (from 20 to 25 °C) did not; all pulses had the same heat unit (°C × time (minutes) = 3600 °C/minute). These results suggest that budbreak of purple nutsedge tubers responds to high temperature as a trigger action.

Varying degrees of tuber dormancy cause irregular emergence of purple nutsedge and greatly contribute toward its persistence as a weed. An understanding of tuber dormancy and sprouting is prerequisite to predicting or manipulating emergence and simplifying management options.

The sprouting of buds on individual purple nutsedge tubers is strongly regulated by soil temperature (Miles, 1991; Miles et al., 1996; Tripathi, 1967; Ueki, 1969). The minimum, maximum, and optimum constant temperatures for purple nutsedge sprouting were 10 to 13 °C, 44 to 45 °C, and 30 to 35 °C, respectively (Holt and Orcutt, 1996; Miles, 1991; Tripathi, 1967; Ueki, 1969). Although most studies used constant temperature to determine sprouting, it is clear that fluctuating temperature caused more sprouting (Miles, 1991; Miles et al., 1996; Tripathi, 1967). Daily fluctuating temperatures of 25 and 35 °C caused 100% sprouting (Miles et al., 1996), while sprouting at constant temperature regimes from 10 to 45 °C never achieved 100% sprouting (Miles, 1991; Ueki, 1969). Miles (1991) increased sprouting of individual tubers in the field to near 100% by soil solarization and attributed the near-complete sprouting to an increase in the amplitude of the daily fluctuating temperature and the mean temperature.

Purple nutsedge tuber sprouting involves two steps—budbreak and elongation of the emerged bud, and both steps may be thermally regulated (Nishimoto et al., 1995). Budbreak occurred readily for most field-collected tubers when held at a relatively constant temperature (84% at 22 to 24 °C) (Nishimoto et al., 1995). However, only about 10% of the emerged buds elongated >1 cm when tubers were held for 3 weeks at a relatively constant temperature. For those tubers that received daily fluctuating temperatures of 22.5 and 27.5 °C for 12 h each, 98% of the tubers had budbreak and 85% of the buds elongated >1 cm. Thus, daily alternating temperature appears to stimulate budbreak and elongation of the emerged buds.

Understanding the attributes of the alternating temperature function (Totterdell and Roberts, 1980) is prerequisite to studying the mechanism involved in the thermal control of breaking dormancy. The phenology of thermal breaking of seed or bud dormancy has been documented well (Benech Arnold et al., 1990; Downs and Bevington, 1981; Erez et al., 1979; Esashi et al., 1983; Lang, 1965; Powell et al., 1988; Stimart and Ascher, 1981; Thompson and Grime, 1977). Thermal responses can be classified either as thermoperiodic or trigger phenomena. The thermoperiodic response occurs when exposure of dormant seeds or buds to alternating temperatures results in increased germination or sprouting compared with the same mean, but constant, temperature. This rhythmic action requires a number of continual alternating cycles, and the effect of each cycle is additive (Benech Arnold et al., 1990; Esashi et al., 1983; Probert et al., 1989). In contrast, the thermal trigger response occurs when dormant tissues receive a single brief fluctuating temperature, such as a thermal pulse of a few minutes to 2 h in which the temperature abruptly shifts from a low base temperature to a higher, but not extreme, temperature, then returns to the base temperature for the rest of experimental period. The trigger action is brief and need not be repeated once dormancy is broken (Amen, 1968). Shifts to a higher temperature, often for only 2 h in darkness, can break dormancy of seeds of several species, including *Nigella*, *Rumex*, and *Echinochloa crus-galli* (Isikawa, 1957; Taylorson and Dinola, 1989; Taylorson and Hendricks, 1972; Vicente et al., 1968), and buds of *Iris* spp (Halevy et al., 1964). In most cases, however, high temperature and light are required for breaking dormancy (Toole et al., 1955, 1957).

The work being reported focused on budbreak or the dormancy release aspect. The experiments were designed to characterize the effect of fluctuating temperature on budbreak and to determine whether the fluctuating temperature-induced budbreak responded as a trigger action or a rhythmic action.

Materials and Methods

PLANT MATERIAL. Purple nutsedge tubers were obtained from the fields at the Univ. of Hawaii's Waimanalo Research Farm. Eight sprouted tubers were grown in each 11-L pot in an unshaded glasshouse. No artificial light was provided. The medium was composed of 2 peatmoss : 1 vermiculite : 1 perlite (by volume), with 23 g/pot Osmocote (18N–2.6P–9.9K) (Grace Sierra, Milpi-

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¹Graduate research assistant.

²Professor; to whom reprint requests should be addressed.

tas, Calif.) incorporated. An additional 15 g/pot Osmocote was top-dressed after 3 months. The pots were watered three to four times a day to avoid desiccation of extensive growth, especially for 4- to 6-month-old plants. The soil temperature in the center of the pot had a sine-wave pattern with the minimum and maximum temperatures of 23 and 29 °C, respectively. In 6 months, mature black or brown tubers were ready for the experiments.

SELECTION OF DORMANT TUBERS. The pots of tubers were brought to the laboratory, which was held at constant 20 °C. The nonsprouted tubers were separated from the mother plants or sprouted tubers on the rhizome-tuber chain and trimmed of roots and rhizomes within 1 day. Tubers were placed in the dark on two layers of filter paper, moistened with deionized water, in 15-cm petri dishes enclosed in a clear polyethylene bag. After incubation at 20 °C for 2 weeks, the nonsprouted tubers were considered dormant and were used in the following experiments. Budbreak occurred readily at constant 20 °C, approaching an asymptote at about 75% after 2 weeks (Nishimoto et al., 1995); thus, typically only about 25% of the normal tuber population was used.

EVALUATION OF TEMPERATURE EFFECT. In each experiment, 10 nonsprouted tubers were placed on two layers of filter paper moistened with 2 mL deionized water in 9-cm Petri dishes enclosed in a polyethylene bag and treated for 7 d. Budbreak was recorded when one or more emerged buds were visible. Budbreak was based on the number of tubers with budbreak over viable tubers in each petri dish. Tuber viability was tested by incubating the nonsprouted tubers at alternating temperatures of 20 and 35 °C for 12 h at each temperature for 1 week; if tubers still did not have budbreak, they were treated with triphenyl tetrazolium chloride (TTC) and examined as described by Miles et al. (1996). In most cases, the viability of the tuber population was about 100%.

NUMBER OF HIGH TEMPERATURE PULSES. The base temperature of 20 °C and high pulse temperature of 35 °C was chosen as the standard dormancy-breaking treatment (Miles et al., 1996). The 30-min pulse of 35 °C temperature was supplied by transferring tubers from an incubator set at 20 ± 1 °C to an incubator set at 35 ± 1.0 °C for 30 min, then returning them to the incubator at 20 °C in the dark. It took about 30 min for the tuber's surface temperature to reach 35 °C from 20 °C in the incubator at 35 °C. The tuber surface temperature was measured by attaching thermocouples on the tuber surface. Pulses were provided one, two, four, or seven times at the beginning of each consecutive 24-h period.

Fig. 1. Budbreak of purple nutsedge tubers in response to increasing numbers of thermal pulses (35 °C for 30 min). All tubers were kept at constant 20 °C between pulses. Horizontal bars represent ± SE. Bars with different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

DURATION OF A SINGLE HIGH-TEMPERATURE PULSE. Nonsprouted tubers were exposed to a single 35 °C pulse of 0, 0.5, 1, 3, 6, or 12 h, then returned to the incubator set at 20 °C for 7 d. In the same experiment, nonsprouted tubers were placed in an incubator set at 55 °C, and, after 3 min, the nonsprouted tubers were returned to the incubator set at 20 °C. It took 3 min for the tuber surface temperature to reach 35 °C, and this treatment was referred to as a 3-min 35 °C pulse.

RAPID VERSUS GRADUAL SHIFT. To evaluate the effect of the rate of temperature change, a sine-wave temperature curve was obtained by using dry sand as a heat buffer. The petri dishes containing tubers on two layers of moistened paper and enclosed with a polyethylene bag were buried 15 cm below the surface of sand in a foam container (26 × 36 × 30 cm) filled with dry sand to a depth of 20 cm. The foam container was transferred to an incubator set at 20 °C. At transfer, the incubator temperature was reset to 49 °C for 12 h, then 6 °C for 12 h; air temperature changed at about 0.5 °C per min until the set temperature was reached. As a result, the tuber temperature gradually increased from 20 to 35 °C in 12 h, then slowly decreased to 20 °C in 12 h. Thereafter, the petri dishes were transferred into an incubator set at 20 °C for 6 d. A single rapid shift was obtained by moving nonsprouted tubers from an incubator set at 20 °C to one set at 35 °C for 12 h, then back to the incubator

Fig. 2. Effect of duration at 35 °C in a single thermal fluctuation (A) and a 3-min 35 °C pulse (B) on budbreak of purple nutsedge tubers. The 3-min 35 °C pulse was achieved by incubation in a 55 °C incubator for 3 min, when tuber surface temperature reached 35 °C. After the treatment, tubers were returned to constant 20 °C. The value for sprouting at constant 20 °C is at 0 h at 35 °C period. Horizontal bars represent ± SE. Bars with different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

set at 20 °C for 6.5 d. A daily rapid shift was achieved by repeating the single rapid shift seven times.

LOW- VERSUS HIGH-TEMPERATURE PULSE. Nonsprouted tubers were selected after incubation at 25 °C for 2 weeks, and 25 °C was used as the base temperature for this experiment instead of 20 °C in all other experiments. Tubers were exposed to 15 °C for 12 h (low temperature) or to 35 °C for 12 h (high temperature) then returned to 25 °C. The number of tubers with budbreak was recorded at 5 d.

MAGNITUDE OF WARM TEMPERATURE PULSE. To eliminate the cumulative influence of temperature on budbreak, different exposure times from 3 to 12 h, but with the same heat units (3600 °C min), were used. Nonsprouted tubers held at a base temperature of 20 °C were exposed to a single pulse of 25 °C for 12 h, 30 °C for 6 h, 35 °C for 4 h, or 40 °C for 3 h, then returned to constant 20 °C, so that each treatment was equivalent in heat units [$^{\circ}\text{C} > 20^{\circ}\text{C} \times \text{time (min)} = 3600^{\circ}\text{C/min}$]. In another set of treatments, nonsprouted tubers were exposed to 30, 35, or 40 °C for 30 min, then returned to constant 20 °C. In both experiments, treatments were compared to the constant 20 °C control.

STATISTICAL ANALYSIS. A completely randomized design was used for each experiment, with four replicated dishes of 10 tubers per treatment, and each experiment was conducted at least twice. Results between treatments did not differ between replicated experiments, although the percent budbreak values for the same treatment sometimes varied between experiments, and data from only one are shown. The number of sprouted tubers in a petri dish was transformed to a percentage before statistical analysis. Percentage data were not binomially distributed and were subjected to analysis of variance without transformation. Duncan's multiple range test was used for mean separation.

Results

NUMBER OF HIGH-TEMPERATURE PULSES. Only 25% of purple nutsedge tubers had budbreak when incubated at constant temperature of 20 °C for 7 d, whereas a single 30 min temperature pulse at 35 °C increased the budbreak to 80% or higher; a single pulse was as effective as seven pulses (Fig. 1).

DURATION OF A SINGLE HIGH-TEMPERATURE PULSE. Although a single 30-min pulse at 35 °C was as effective as seven cycles, 10% to 20% of the tubers remained unsprouted. To determine whether nonsprouted tubers needed a longer period of high temperature for budbreak, tubers were exposed to different durations at 35 °C.

Fig. 3. Effect of rate of temperature change from 20 to 35 °C on budbreak of purple nutsedge tubers. The rate of temperature change was 0.5 and 0.02 °C per min, for the rapid and gradual shift, respectively. Horizontal bars represent $\pm$ SE. Bars with different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

Budbreak was not increased by exposing tubers to 35 °C for longer than 30 min (Fig. 2A). Although 30 min of incubation at 35 °C broke dormancy, tubers remained at 35 °C only for a few min, as 30 min was required for the tuber surface to reach this temperature. A 3-min incubation at 55 °C was used to raise the tuber temperature to 35 °C from 20 °C, and this induced 63% sprouting versus 20% for constant 20 °C (Fig. 2B).

RAPID VERSUS GRADUAL SHIFT. Transferring tubers directly from 20 to 35 °C resulted in a change in tuber surface temperature of 0.5 °C per min, while the rate in the sand-buffered condition was 0.02 °C per min. However, both treatments resulted in similar budbreak, which was not different from budbreak with the daily rapid shifts, but greater than that at constant 20 °C (Fig. 3).

LOW- VERSUS HIGH-TEMPERATURE PULSE. Budbreak of dormant tubers at constant 25 °C was 55% (Fig. 4), which, as expected, was higher than at 20 °C (Fig. 3). Raising the temperature (35 °C for 12 h) stimulated sprouting, whereas lowering it (15 °C for 12 h) elicited the same extent of sprouting as at constant 25 °C (Fig. 4).

MAGNITUDE OF WARM TEMPERATURE PULSE. A shift of 5 °C from 20 to 25 °C had no effect on budbreak, while shifts of 10 °C or greater promoted budbreak (Fig. 5A). Increasing the maximum temperature from 30 to 40 °C did not increase budbreak further. In the 30-min heat treatments, 30, 35, and 40 °C pulses induced more budbreak than constant 20 °C, but, again, there was no significant difference among the heat treatments (Fig. 5B).

Discussion

About 75% budbreak of purple nutsedge tubers occurs without any high-temperature stimuli (Nishimoto et al., 1995), and this study focused on the remaining 25% that was dormant. Dormancy can be broken by many stimuli such as dry-air storage, light, and temperature (Amen, 1968). The effectiveness of stimuli varies with plant species. For purple nutsedge tubers, one shift in temperature from 20 to 35 °C for 12 h induced >92% budbreak and was as effective as seven daily alternations (Fig. 3). Furthermore, a single 30-min exposure to 35 °C was equivalent to seven daily cycles (Fig. 1). These results show that one short exposure to high temperature is sufficient to break dormancy. In fact, only a few minutes of high temperature (35 °C) could stimulate budbreak (Fig. 2B), indicating that recognition and reception of the thermal signal by tuber cells were very rapid and that the transduction of the external thermal signal to intermolecular chemical or biochemical messengers may be irreversible. However, the 3-min pulse to 35

Fig. 4. Effect of increase versus decrease in temperature on budbreak of purple nutsedge tubers 5 d after treatment. In this experiment, constant 25 °C was used instead of constant 20 °C for preincubation and selection of dormant tubers and for the base temperature in both temperature shifts. Horizontal bars represent $\pm$ SE. Bars with different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

Fig. 5. Effect of magnitude of a single temperature shift on budbreak of purple nutsedge tubers. Each long-duration treatment (A) was equivalent in heat units ($^{\circ}\text{C} > 20^{\circ}\text{C} \times \text{time (min)} = 3600^{\circ}\text{C}/\text{min}$). In the 30-min pulse treatments (B), tubers were exposed to the high temperature for 30 min. Horizontal bars represent $\pm$ SE. Bars with different letters differ significantly by Duncan's multiple range test, $P = 0.05$.

$^{\circ}\text{C}$ appeared to be less effective than the 30-min pulse (Fig. 2 A and B), possibly because of the lack of uniform heat transfer when rapidly heating tubers in a few minutes (Taylorson and Hendricks, 1972). Taken together, our data suggest that high temperature acts as a trigger or a switch, rather than rhythmic phenomena. The requirement for a short exposure to high temperature to induce budbreak could explain how a tuber population from the field produced budbreak readily (84%) when incubated at room temperature (22 to 24 $^{\circ}\text{C}$) (Nishimoto et al., 1995). The budbreak could partly be induced by exposure to high temperatures during the collection and handling process, as daily air temperature in the field typically varies from 20 to 32 $^{\circ}\text{C}$.

Daily alternating temperatures consistently resulted in 100% budbreak (Fig. 3) and subsequent shoot elongation (Miles et al., 1996). A single exposure to 35 $^{\circ}\text{C}$ for 30 min usually does not cause 100% budbreak within 1 week (Figs. 1 and 2A). Incubation of thermal pulse-treated tubers at constant 20 $^{\circ}\text{C}$ for another week gradually increased sprouting, but a few viable tubers remained unspouted (data not reported). Neither additional 30-min pulses nor prolonging the duration of high temperatures in a single shift induced 100% budbreak. However, a combination of providing daily exposures and prolonging their duration from 30 min to 12 h increased budbreak to 100% (Fig. 3).

Raising the temperature from 25 to 35 $^{\circ}\text{C}$ for 12 h induced budbreak, while lowering it from 25 to 15 $^{\circ}\text{C}$ for 12 h had no effect (Fig. 4), indicating that the rise in temperature was more important than the drop in temperature. The critical factor was the magnitude of the rise. When tuber temperature increased 10 $^{\circ}\text{C}$ or more above the

base temperature 20 $^{\circ}\text{C}$, dormancy was broken. This characteristic is similar to a heat-shock response. The heat-shock temperature is generally 8 to 10 $^{\circ}\text{C}$ above the normal growing temperature (Key, 1992). The temperature of 20 $^{\circ}\text{C}$ was considered a suitable condition for the purple nutsedge budbreak since about 75% budbreak occurs when freshly harvested tubers are incubated at constant 20 $^{\circ}\text{C}$ (Nishimoto et al., 1995). Our 15 $^{\circ}\text{C}$ temperature increase emulates conditions reported to cause heat shock, and heat-shock proteins may be involved in the thermal signal transduction and regulation of dormancy release in purple nutsedge tubers.

Brief exposures to an elevated temperature stimulate budbreak of tubers in the laboratory and probably are important in triggering budbreak of purple nutsedge tubers in the field. In addition, the fact that the rate of temperature change was not critical for budbreak (Fig. 3) suggests that gradual increases in temperature that occur in natural soil could serve as the stimulus for budbreak of purple nutsedge tubers in the field.

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