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Increased Purple Nutsedge (*Cyperus rotundus*) Tuber Sprouting with Diurnally Fluctuating Temperatures

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Purple nutsedge is among the most troublesome weeds of vegetables in the Southeast US and a substantial impediment in the search for methyl bromide alternatives. Greater understanding of the environmental cues that regulate tuber sprouting may assist in improved nutsedge management. Experiments were conducted to evaluate the effect of diurnal temperature variation on sprouting of purple nutsedge tubers. Two temperature regimes were evaluated: the first averaged 28 C, with daily fluctuations ranging from 0 to 19.5 C; the second temperature regime averaged 16 C, with daily fluctuations ranging from 0 to 18.5 C. When average temperature was 28 C, cumulative tuber sprouting ranged from 88 to 92%, with no detectable differences among diurnal fluctuations. The high average temperature in the first study may have negated any type of enforced sprouting suppression. However, when average temperature was lowered to 16 C (simulating early spring diurnal fluctuations under polyethylene mulch), there was a positive linear correlation between maximum tuber sprouting and temperature variation. With an average temperature of 16 C, the absence of temperature variation resulted in 52% purple nutsedge sprouting, while 87% sprouting occurred when daily temperature varied 18.5 C at the same average temperature. The use of various types of mulching material can affect average soil temperatures and diurnal variations, potentially shifting nutsedge emergence. Further studies are needed to determine if these data on tuber sprouting in response to alternating temperatures can facilitate more efficient weed management.

Nomenclature: Purple nutsedge, *Cyperus rotundus* L. CYPRO.
Key words: Alternating temperatures, germination, vegetative propagule.

Suspected to be a weed by the first century A.D. (Negbi 1992), purple nutsedge continues to be an economic threat to vegetable crop production around the world, including the southeast United States (Webster 2010). Purple nutsedge is a perennial that can reproduce sexually from seed and asexually from tubers. As the seeds have low viability (Justice and Whitehead 1946), tubers are the primary method of reproduction (Wills 1987). Purple nutsedge tubers are spread out along the rhizomes that grow from the primary tuber, with a single tuber producing 34 tubers in 10 wk of growth (Webster et al. 2008). Many of the tubers in the rhizome chain are suppressed through apical dominance; when the chain is broken through mechanical means (i.e. tillage or cultivation) the dominance is no longer expressed, and the previously dormant tubers will sprout (Muzik and Cruzado 1953; Smith and Fick 1937).

Until recently, high-value vegetable production in the southeast United States used methyl bromide to control a multitude of pests, including plant pathogens, soil borne insects, nematodes, and weeds (Csinos et al. 2002; Gilreath and Santos 2005; Schneider et al. 2003; Webster et al. 2001). However, use of methyl bromide has been eliminated as a fumigant for vegetable production due to concerns that it is an ozone-depleting substance, with exception to critical use exemptions that are granted by the Methyl Bromide Technical Options Committee of the United Nations. As growers transition from methyl bromide to alternative fumigants, purple nutsedge has become a more common weed in Georgia vegetables, from the tenth most common weed in 1999 (Dowler 1999) to the most troublesome weed of fruiting vegetables (e.g., solanaceous crops) and cucurbits in 2010 (Webster 2010). This weed shift necessitates a greater understanding of the biology and physiology of purple nutsedge to improve management tactics.

Purple nutsedge shoots possess a sharp point in the absence of light, which allows it to readily pierce polyethylene mulch used in vegetable production (Chase et al. 1998; Patterson 1998). Webster (2005) reported that under black-opaque low-density polyethylene mulch, a single tuber can multiply to a patch of 3,440 shoots over an area of 22 m^2 in 60 wk. Nutsedge growth through the polyethylene mulch barrier competes with the crop for nutrients and water that is supplied through drip irrigation (Santos et al. 1997; William and Warren 1975) and degrades mulch integrity, limiting the ability to use mulch over multiple crops and growing seasons (Johnson et al. 2007).

Diurnal variations in temperature stimulate seed germination in many species (Morinaga 1926; Thompson and Grime 1983; Thompson et al. 1977). Johnsongrass [*Sorghum halepense* (L.) Pers.] seed germination declined with temperature variation, suggesting a potential mechanism for the seed to detect soil depth and maximize successful establishment opportunities (Ghersa et al. 1992). While purple nutsedge shoots sprout from tubers with large energy reserves relative to seeds, emerged shoots disappear in the shade of a crop canopy and new shoots do not readily emerge. One potential mechanism for this shade avoidance strategy in regulating shoot emergence could be dampened diurnal temperature fluctuations. Grower understanding of temperature influence on nutsedge emergence used alone or in combination with the shade avoidance strategy could be used as part of a pest management program.

To identify the effects of diurnal temperature effects, different ranges of temperature variance were chosen and nutsedge tuber sprouting was evaluated using a thermogradient. Experiments were conducted to determine if temperature fluctuations affected purple nutsedge sprouting, while holding all other variables constant. As soil composition and tuber burial depth would be additional variables, it was

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Table 1. Treatment structure of the alternating temperatures including: the diurnal fluctuation between the maximum and minimum temperatures, the durations of the temperatures for each treatment, and the mean daily temperature.

Study 1			Study 2					
Mean temperature 28.3 C			Mean temperature 16.1 C			Mean temperature 16.2 C		
Fluctuation	16 h	8 h	Fluctuation	16 h	8 h	Fluctuation	16 h	8 h
0.0	28.3	28.3	0.0	16.1	16.1	0	16.2	16.2
4.0	30.0	26.0	2.6	15.4	18.0	2.3	15.5	17.8
9.0	32.0	23.0	4.0	15.2	19.2	3.1	15.3	18.4
14.5	33.0	18.5	5.6	14.4	20.0	4.4	15.0	19.4
19.5	35.5	16.0	7.7	13.8	21.5	5.9	14.3	20.2
			12.2	12.0	24.2	8.9	13.4	22.3
			18.5	10.4	28.9	11.8	12.5	24.3
						15.7	11.0	26.7
						16.8	10.6	27.4

decided to conduct the experiment in a laboratory setting where diurnal temperature fluctuations and growing degree days could be controlled and compared.

Materials and Methods

Plant Materials. Purple nutsedge tubers were collected from a field at the USDA-ARS Jones Research farm near Chula, GA (31° 30.79′N, 83° 32.65′W) on September 14, September 23, and October 27 in 2008; January 7 and January 24, 2009; March 29, 2010; and February 16, 2011. These tubers were harvested using a field cultivator to move plant material to the field edge, after which tubers were separated from chains by hand. Tubers selected for this study were of uniform size, approximately 1.2 cm long, 0.75 cm wide, with a fresh biomass of 1.1 g and did not possess aerial shoots. Purple nutsedge tubers were collected and used either on the day of, or within 3 d of digging; tubers were kept at 4 C until trial initiation. Each experimental unit consisted of 25 tubers placed on a blotter disk (Anchor Steel Blue Germination Blotter Paper, SDB3.5, Anchor Paper Company 480 Broadway, St. Paul, Minnesota 55101) in a Petri dish (extra-deep, disposable polystyrene dishes, diam, 10 cm; height 2 cm, Fischer Scientific, 200 Park Lane, Pittsburgh, PA 15275). Deionized water (10 ml) was added to each dish, and replenished when necessary, for the duration of the experiment. Dishes were then placed on a thermogradient table with nine experimental units for each diurnal temperature variation.

Thermogradient. Purple nutsedge tuber response to temperature and time for sprouting were evaluated on a thermogradient table (Cardina and Hook 1989; Grey et al. 2011; Webster and Cardina 1999). The table was constructed from a solid aluminum block measuring 2.4 m long by 0.9 m wide by 7.6 cm thick with a mass of 470 kg. On either end of the aluminum block, a 1.0 cm hole was drilled across the side section to allow fluid to be pumped into the table. On either end of the table, chilled or heated ethylene glycol plus water (1 : 10 mixture) were pumped at 3.8 L min^{-1} to generate the thermogradient. Along the length of the thermogradient a variation in temperature occurred, with a constant temperature across the width. This allowed for 24 increments across the length to obtain different temperatures, with nine increments across the width at each temperature.

Thermocouples made from duplex insulated wire (Insulated PR-T-24 wire, Omega Engineering, Inc Stamford, CT 06907-2336) were mounted to the underside of the table from the chilled to heated ends directly under each Petri dish. Each thermocouple was placed into tubing measuring 8 cm long, 4.8 mm inside diameter, and 7.9 mm outside diameter. This was then inserted vertically into a hole on the underside of the table. Holes measured 8 mm wide by 7 cm deep to allow the thermocouple to be within 0.5 cm of the upper table surface, at 10-cm intervals along the length of the table. Temperature for each Petri dish was monitored continuously for each thermocouple and recorded by a data logger (Graphtec Midi Logger, GRAPHTEC Corporation, 503-10 Shinano-cho, Totsuka-ku Yokohama 244-8503, Japan) at 30-min intervals; temperature data for each thermocouple was downloaded daily.

Temperature Variation. Two different studies were conducted. Purple nutsedge tubers collected on the first three sample dates, September 14, September 23, and October 27 in 2008, comprised the three repetitions of the first study, while tubers collected at the four later dates, January 7 and January 24, 2009; March 29, 2010; and February 16, 2011, comprised the four repetitions of the second study. Purple nutsedge tubers in Petri dishes were exposed to16 h of one temperature and then moved to a separate cell for 8 h of another temperature. All dishes accumulated the same growing degree days (GDD) though there were several distinct levels of variation in temperature between warm and cool (Table 1). Average temperature in the first study was 28 C, while the second study average temperature was 16 C. Different thermal gradient tables were used in the first two and second two repetitions of the studies with the average temperature of 16 C, so there were slight differences in temperature fluctuations (Table 1). Dishes were evaluated every 24 h for 8 d and tubers with a root or shoot emerged at least 5 mm were counted and removed from the dish. The GDD were calculated using a base temperature of 10.4 C (Holt and Orcutt 1996), which was subtracted from the daily average temperature recorded for each experimental unit. To reflect the amount of GDD accumulated over a twenty-four hour period, the resulting equation is:

$$GDD = [(T_{8h} - T_{Base})(8h/24h)] + [(T_{16h} - T_{Base})(16h/24h)] \quad [1]$$

Where T_{8h} is the average temperature during the 8 h portion of the diurnal fluctuation for each treatment and T_{16h} is the average temperature for the 16 h portion of the diurnal treatment. When average temperature was 28 C, the T_{8h} corresponded to the cooler temperature and the T_{16h} to the

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Table 2. Parameter estimates and 95% confidence interval (CI)[a] for sprouting of purple nutsedge when varying temperature using a thermogradient with average temperature of 28.3 C, exposing tubers to 16 hours of warm then 8 hours of cool diurnal cycles.

	Parameter a[b]			Parameter b_1[b]			Parameter b_2[b]		
Temperature variation	Maximum germination	95% CI		Estimate	95% CI		Estimate	95% CI	
0	87.8	±11.8	a	4.7	±7.4	NS	0.10	±0.04	a
4.3	92.0	±8.8	a	4.1	±5.9	NS	0.08	±0.04	a
9.4	92.1	±5.7	a	2.1	±2.6	NS	0.10	±0.03	a
14.5	90.0	±5.7	a	1.5	±2.2	NS	0.10	±0.03	a
19.5	90.1	±6.1	a	1.3	±2.2	NS	0.10	±0.04	a

[a] Parameter estimates calculated by nonlinear regression equation, $y = a/\left(1+((a-b_1)/b_1)\left(e^{(-b_2x)}\right)\right)$, describing the relationship between purple nutsedge tuber sprouting accumulation of growing degree days. Parameter a is the height of the horizontal asymptote at a very large x; Parameter b_1 is the expected value of y (cumulative germination) at time $x = 0$; Parameter b_2 is a measure of growth rate.

[b] Values for each parameter within a column for each temperature variation followed by the same letter are not significantly different at the 5% probability level. General linear models procedures were used with mean separation using 95% asymptotic confidence intervals. NS indicates that the parameter estimate is not different from zero.

warmer temperature, while in the 16 C average temperature, the T_{8h} was the warmer temperature and the T_{16h} the cooler temperature.

Purple nutsedge tuber sprouting as a function of growing degree days (x) was fit to a nonlinear regression model equation:

$$y = a/\left(1+((a-b_1)/b_1)\left(e^{(-b_2x)}\right)\right) \quad [2]$$

For the equation, a is the height of horizontal asymptote at a very large x, b_1 is the expected value of y at time $x = 0$, b_2 is the measure of growth rate. This is a modified version of the equation described by Chen and Nelson (2006) and applied to seed germination by Grey et al. (2011). Data were combined and analyzed across repetitions of the studies for the 28 C, with the first two and last two repetitions the 16 C analyzed separately due to the differences in treatments. A mixed model analysis was used where repetitions of the studies were considered a random effect (SAS 9.2, SAS Institute, Inc., Cary, NC USA 27513-2414). General linear models procedures were used with mean separation using 95% asymptotic confidence intervals.

Results and Discussion

First Experiment: 28 C Mean Temperature. Purple nutsedge emergence at each of the diurnal temperature fluctuations (average diurnal temperature of 28 C) were described by a logistic regression model, but there were no differences in parameter estimates among the temperature variations (Table 2). Purple nutsedge tubers held at a constant temperature at 28 C had a maximum cumulative sprouting of 88%, while diurnal variations at this average temperature of 4, 9, 15, and 23 C had maximum cumulative sprouting rates between 90 and 92%. Miles et al. (1996) determined sprouting of dormant purple nutsedge tuber increased with temperature fluctuation. Their experiment utilized an incubator with diurnal fluctuations of 0 (constant temperature), 2, 4, and 6 C, but mean temperatures ranged from 21 to 24 C (Miles et al. 1996). In contrast, all tubers in the current study accumulated the same number of growing degree days, with diurnal fluctuations as the only treatment difference. Another study conducted in Greece reported that purple nutsedge tuber sprouting increased as temperature fluctuations increased from 0 to 12 C (Travlos et al. 2009). In the study by Travlos et al. (2009), average temperature for each treatment was held constant at 32 C. However, while mid-summer daily average soil temperatures under polyethylene mulch can exceed 35 C in our location (Johnson et al. 2007; Webster 2003), nutsedge emergence typically occurs in the spring before these temperatures are achieved.

A potential source of variation between the current study and that of Travlos et al. (2009) was the selection of tubers used in the studies. In the current study, nutsedge tubers were selected to be as uniform as possible. In contrast, Travlos et al. (2009) used tubers sampled from two different depths, 0 to 5 cm and 5 to 15 cm. Tubers from these depths had different average dry biomass (0.12 g at 0 to 5 cm and 0.17 to 0.24 g at

Table 3. Parameter estimates and 95% confidence interval (CI) for sprouting of purple nutsedge when varying temperature using a thermogradient with average temperature of 16.1 C, exposing tubers to 16 hours of cool then 8 h of warm diurnal cycles[a].

	Parameter a[b]			Parameter b_1[b]			Parameter b_2[b]		
Temperature variation	Maximum germination	95% CI[b]		Estimate	95% CI		Estimate	95% CI	
0	52.2	±3.2	c	0.88	±0.40	a	0.11	±0.010	b
2.6	69.3	±8.3	b	1.1	±0.42	a	0.09	±0.010	c
4.0	78.0	±1.1	b	1.3	±0.45	a	0.09	±0.001	c
5.6	69.2	±3.8	b	1.6	±0.57	a	0.11	±0.010	b
7.7	70.6	±3.1	b	0.83	±0.28	a	0.11	±0.010	b
12.2	85.2	±1.9	a	1.2	±0.30	a	0.12	±0.008	b
18.5	87.1	±1.1	a	0.36	±0.11	b	0.18	±0.010	a

[a] Parameter estimates calculated by nonlinear regression equation, $y = a/\left(1+((a-b_1)/b_1)\left(e^{(-b_2x)}\right)\right)$, describing the relationship between purple nutsedge tuber sprouting accumulation of growing degree days. Parameter a is the height of the horizontal asymptote at a very large x; Parameter b_1 is the expected value of y (cumulative germination) at time $x = 0$; Parameter b_2 is a measure of growth rate.

[b] Values for each parameter within a column for each temperature variation followed by the same letter are not significantly different at the 5% probability level. General linear models procedures were used with mean separation using 95% asymptotic confidence intervals.

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Table 4. Parameter estimates and 95% confidence interval (CI) for sprouting of purple nutsedge when varying temperature using a thermogradient with average temperature of 16.2 C, exposing tubers to 16 hours of cool then 8 hours of warm diurnal cycles[a].

Temperature variation	Parameter a[b]			Parameter b_1[b]			Parameter b_2[b]		
	Maximum germination	95% CI		Estimate	95% CI		Estimate	95% CI	
0	50.9	±8.8	d	0.05	±0.64	NS	0.15	±0.048	a
2.3	68.7	±8.8	bc	0.45	±0.76	NS	0.18	±0.067	a
3.1	60.4	±12.7	cd	0.26	±0.51	NS	0.17	±0.069	a
4.4	70.4	±7.1	bc	0.21	±0.27	NS	0.19	±0.047	a
5.9	63.8	±11.0	cd	0.49	±0.64	NS	0.15	±0.049	a
8.9	89.6	±7.0	a	0.24	±0.24	NS	0.19	±0.035	a
11.8	88.1	±8.5	a	0.24	±0.35	NS	0.20	±0.053	a
15.7	93.1	±5.0	a	0.10	±0.11	NS	0.23	±0.041	a
16.8	87.3	±10.7	ab	0.23	±0.30	NS	0.19	±0.046	a

[a] Parameter estimates calculated by nonlinear regression equation, $y = a/\left(1+((a-b_1)/b_1)\left(e^{(-b_2 x)}\right)\right)$, describing the relationship between purple nutsedge tuber sprouting accumulation of growing degree days. Parameter a is the height of the horizontal asymptote at a very large x; Parameter b_1 is the expected value of y (cumulative germination) at time $x = 0$; Parameter b_2 is a measure of growth rate.

[b] Values for each parameter within a column for each temperature variation followed by the same letter are not significantly different at the 5% probability level. General linear models procedures were used with mean separation using 95% asymptotic confidence intervals. NS indicates that the parameter estimate is not different from zero.

5 to 15 cm) and sprouting characteristics (Travlos et al. 2009). A previous study reported a linear relationship between tuber weight and tuber sprouting (Kawabata and Nishimoto 2003). In addition, while uniform tuber size used in the current study may have assisted in eliminating some of the variability in temperature response due to tuber age and/or amount of reserves, it may provide a less realistic *in situ* response of the propagule-bank relative to the Travlos et al. (2009) sampling method.

Second Experiment: 16 C Mean Temperature. When average daily temperature was reduced to 16 C, there were treatment effects when purple nutsedge tubers were subjected to diurnal temperature fluctuations ranging from 0 to 18.5 C (Tables 3 and 4). Logistic regression models described the relationship between tuber sprouting and time for each of the unique diurnal temperature fluctuations (Tables 3 and 4). There were no consistent differences in parameters b_1 (x-intercept) or b_2 (tuber sprouting rate) among the temperature variation treatments, which is consistent with previous applications of this equation (Chen and Nelson 2006; Grey et al. 2011). At a constant 16 C, the predicted maximum sprouting (parameter *a*) was 52%, with this parameter approaching 90% at the maximum diurnal fluctuations evaluated in this study. There was a positive correlation ($r = 0.86$, $P < 0.0001$) between maximum sprouting (parameter *a*) and temperature variations when the mean daily temperature was 16 C (Figure 1). This confirms previous research conclusions that tuber sprouting is regulated by alternating diurnal temperatures (Miles et al. 1996; Travlos et al. 2009). However, the current research demonstrates that this phenomenon occurs at temperatures common during initiation of spring vegetable production in the southeast US, temperatures lower than previously tested. The purple nutsedge tubers used in this study were adapted to Georgia environmental conditions, and responded to temperature fluctuations similar to those experienced in the early spring when aerial shoots of nutsedge tubers begin to emerge. Kawabata and Nishimoto (2003) observed differential responses to temperature of purple nutsedge tubers collected from various latitudes. Locales near the equator have less daily temperature fluctuation; data revealed that tubers collected from lower latitudes had greater dormancy and were less responsive to fluctuating temperatures (Kawabata and Nishimoto 2003). The current experiment was conducted on tubers collected from latitude 31.51°N, while the Travlos (2009) study used tubers from latitude 37.97°N, explaining some of the differences observed between these studies.

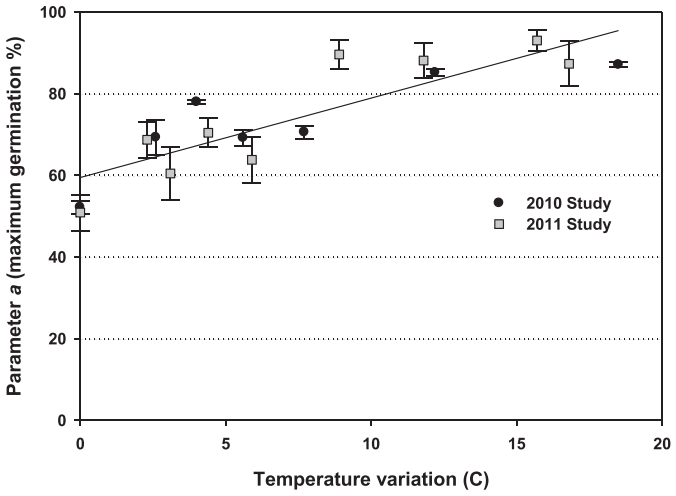


Figure 1. The correlation between maximum tuber sprouting (parameter *a* estimates from Tables 2 and 3) and temperature fluctuation when average temperature was maintained at 16 C; y = 57.5 + 2.25x, ($r = 0.89$, $P = 0.00128$).

In the absence of methyl bromide, varied control measures are being investigated to improve nutsedge management. Effective herbicide tools for controlling purple nutsedge in vegetable crops are limited and often complicated by crop tolerance and herbicide persistence on polyethylene mulch (Culpepper et al. 2009; Grey et al. 2007; Grey et al. 2009; Webster et al. 2003). Therefore, growers must utilize practices that do not rely solely on herbicides. Soil preparation for vegetable production in Georgia typically occurs between January and March, when soil temperatures are more moderate (11 to 15 C) (Hoogenboom 2011) than those (32 C) used by Travlos et al. (2009). Diurnal soil temperature variations in March 2006 in Tifton, GA were 15.9 C under black polyethylene mulch, 13.4 C without mulch, and 8.7 C under silver-reflective mulch (Webster, unpublished data).

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One potential application of the data in this study is development of practices that increase diurnal fluctuations to stimulate purple nutsedge sprouting in coordination with effective herbicide-based programs prior to crop transplant. This may require a change in timing of soil preparation and polyethylene mulch covered bed formation in the winter. Alternatively, cultural practices that suppress diurnal fluctuations until a crop canopy can establish (and shade the low-growing purple nutsedge plants), may have potential to minimize purple nutsedge sprouting and establishment. Effective management of purple nutsedge requires a coordinated effort among multiple tactics that minimize purple nutsedge establishment, growth, and reproduction.

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