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Wetland Nightshade (*Solanum tampicense*) Growth Response to Temperature, and Winter Survival, in Relation to Potential Spread[1]

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Abstract: Greenhouse, growth chamber, and winter survival studies were conducted at Stoneville, MS from 1996 to 2002 to determine growth, time to first flower, and winter survival of wetland nightshade. At 12 wk after emergence, wetland nightshade plants had 58-, 45-, 48-, and 4-cm heights, respectively; 24, 21, 21, and 12 nodes/plant, respectively; 62, 31, 36, and 21 leaves/plant, respectively; and 7.1, 3.9, 5.1, and 0.3 g/plant dry weights, respectively, at temperatures of 26/36, 20/30, 14/24, and 8/18 ($\pm$0.5) C at the 14/10 day/night length. Flowering occurred at 79, 85, and 85 days after emergence at 26/36, 20/30, and 14/24 C night/day, respectively at the 14/10 day/night cycle. Wetland nightshade plants did not flower at 8/18 C. Wetland nightshade growth was adequate for flowering and fruit production in additional areas of the southeastern United States with night/day temperatures greater than or equal to 14/24 C. Winter survival was greater than or equal to 33% for established wetland nightshade plants in 5 of 6(1996 to 2002) above water levels and 82% from 20 cm below the water surface. Based on these results, wetland nightshade has the potential to continue to spread in the United States.

Nomenclature: Wetland nightshade, *Solanum tampicense* Dunal #[3].

Additional index words: *Solanum tampicense* Dunal.

INTRODUCTION

Wetland nightshade is a member of the section *Micrantha* of family Solanaceae (M. Nee, personal communication). It is a perennial shrub of warm climates and high-rainfall tropical regions. In some texts, wetland nightshade has been incorrectly referred to as *S. houstonii* Dunal (Wunderlin et al. 1993). Its closest kin in the United States is Jamaican nightshade (*Solanum jamaicense* P. Mill.), also a nonnative invasive of the section *Micrantha* Wetland nightshade is among several native and nonnative prickly *Solanum* species in the southeastern United States (Bryson and Coile 1999; Fox and Bryson 1998). Wetland nightshade and two other prickly nightshades, tropical soda-apple (*Solanum viarum* Dunal) and turkeyberry (*Solanum torvum* Sw.), are listed as federal noxious weeds (Fox and Bryson 1998; Mullahey et al. 1998). The common names for wetland nightshade include aquatic soda-apple (Fox and Wigginton 1996a, 1996b), Tampico soda-apple (Reimus and Robertson 1995), sosumba in Belize (Gentry and Standley 1974), Ajicón in Cuba, and huistomate or huevo de gato in El Salvador (Standley 1924). Aquatic soda-apple was the common name attached to this plant in Florida soon after tropical soda-apple was recognized as a major problem in the United States. Based on habitat requirements and the size of the fruit, the common name wetland nightshade was deemed more appropriate for this species rather than aquatic soda-apple (Fox and Bryson 1998).

Wetland nightshade is thought to have originated in Central America, southern Mexico, the West Indies, Guatemala, and Cuba (Gentry and Standley 1974; Standley 1924). It was first reported from mainland Florida in a marsh south of Punta Gorda, Charlotte County in 1983 by Wunderlin et al. (1993). Since that time, wetland nightshade has been detected in Florida in Highlands (1985), DeSoto (1991), Lee (1995), and Glades (1996) counties and on Garden Key in the Dry Tortugas in a moist seep area within Fort Jefferson since 1974 (Reimus and Robertson 1995).

Since its introduction into Florida, wetland nightshade has invaded natural areas, reducing biodiversity (Fox and Bryson 1998). Wetland nightshade is found in wetland habitats along streams or in moist areas in cypress domes, but unlike true aquatic species it does not tolerate

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[3] Letters following this symbol are a WSSA-approved computer code from *Composite List of Weeds*, Revised 1989. Available only on computer disk from WSSA, 810 East 10th Street, Lawrence, KS 66044-8897.

continuous flooding (Fox and Bryson 1998). The sprawling stems of mature wetland nightshade plants are up to 5 m long and 2 cm diameter near the base. Wetland nightshade stems produce thickets along waterways, displacing native vegetation and probably reducing biodiversity (Coile 1993). These impenetrable thickets also threaten waterways and adjacent agricultural areas by detaining debris, thus slowing water flow and causing flooding (Fox and Bryson 1998). Wetland nightshade has not been observed in upland areas such as pastures and oak hammocks, where tropical soda-apple, turkeyberry, and other native and nonnative weedy prickly *Solanum* species occur.

In Florida, wetland nightshade is capable of reproducing from seeds, by vegetative regeneration from the root crown, and by propagation from stem sections (Fox and Wigginton 1996b; Fox and Bryson 1998). Shoots have been observed to sprout from pieces of roots in the field, but it is unknown which environmental conditions favor this mechanism of regeneration. Wetland nightshade was observed to sprout under water in the field and in caged studies in Florida. In Florida, flowers and fruit are found throughout the year on plants growing in direct sunlight, with the highest frequency occurring between June and January and between September and January for plants growing in shade. Environmental conditions such as flooding and cold temperatures suppress or delay flower production in the shade. Fruits are 0.6 to 1.0 cm in diameter, red at maturity and contain an average of 35 seeds each (Fox and Bryson 1998). Each wetland nightshade stem in full sun light may produce over 2,300 seeds per year; whereas those in the shade would typically produce only 350 seeds per stem annually (Fox and Wigginton 1996a, 1996b). In Florida, multiple shoots are produced from a plant base following mechanical or freezing damage of stems. Isolated sections of stem, as short as 2.5 cm, are capable of regenerating shoots and adventitious roots when placed in water or on moist soil, provided that they include a leaf scar and associated axillary meristem. Floating shoot sections may not fully develop until the stem section is deposited on moist soil. This response provides an additional dispersal mechanism (Fox and Wigginton 1996a).

In Florida in January of 1997, the above ground stems and leaves of whole stands of wetland nightshade were killed by a single night of temperatures just below freezing (C. T. Bryson and A. M. Fox, personal observation). However, when the leaf litter was removed several days later, wetland nightshade shoots were emerging from stems at ground level (A. M. Fox, personal observation). Similar results were observed during 1997 to 1999 from wetland nightshade plants maintained for 2 to 3 yr in 25-cm-deep soil in outdoor tanks at Gainesville, FL.

The objectives of this research were to determine the growth potential of wetland nightshade at several temperature regimes and the potential of winter survival in climates north of the currently known range (at Stoneville, MS) for wetland nightshade.

MATERIALS AND METHODS

Wetland Nightshade Establishment. Wetland nightshade plants for each of the following experiments were established in the greenhouse in 10-cm-diameter pots in a mixture of a Bosket sandy loam (Mollic Hapludalfs) soil and commercial potting mix[4] at 50/50 v/v. Several seeds were planted per pot to insure simultaneous seedling emergence. Wetland nightshade plants were thinned to one plant per pot at cotyledon growth stage. The greenhouse was maintained at temperatures of 20/30 C night/day.

Wetland Nightshade Winter Survival above Water Level. This study was conducted to determine winter survival of wetland nightshade at Stoneville, MS in Zone 7b of the USDA plant hardiness zone map (Anonymous 2003), with average lowest temperatures of −12 to −15 C. Wetland nightshade plants were established in June each year as stated above. Single plants were transplanted into 25-cm-diameter pots in the previously described soil mixture and maintained in the greenhouse at temperatures of 20/30 C night/day. In October of each year, plants were transferred outside onto tables 1 m tall on a concrete slab. Maximum and minimum mean temperatures for late fall, winter, and early spring months for October through May for the years 1996 to 2002 are presented in Table 1 based on data collected by the USDA World Agriculture Outlook Board Weather Stoneville Field Office, Stoneville, MS.

Three wetland nightshade plants were transferred into the greenhouse at the first of each month for 7 mo (November through May) during 1996 to 1999. From 2000 to 2002, three wetland nightshade plants were transferred into the greenhouse in May. Wetland nightshade plants were maintained in the greenhouse at temperatures of 20/30 C night/day for a minimum of 4 mo or until wetland nightshade regrowth was observed. Following regrowth or at the end of 4 mo, all plants, soil, and pots were autoclaved. Data were subjected to analysis of variance,

[4] Jiffy Mix Plus, a registered trademark of Jiffy Products of America, Inc. 951 Swanson Dr., Batavia, IL 60510-4202.

Table 1. Mean maximum and minimum monthly temperatures (C) and overall monthly average temperatures at Stoneville, MS from 1996–2002.

	Monthly average maximum, minimum, and mean[a] temperature																	
	1996–1997			1997–1998			1998–1999			1999–2000			2000–2001			2001–2002		
Month	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean	Max	Min	Mean
October	24	12	15	24	11	14	28	13	16	27	14	18	27	11	15	24	9	12
November	16	6	9	15	4	7	19	8	12	22	7	9	16	5	8	22	7	9
December	14	4	6	11	2	4	13	4	6	14	2	5	7	3	4	15	5	7
January	10	1	3	13	4	6	14	3	7	13	2	6	9	1	2	13	2	6
February	14	4	7	14	4	6	17	6	9	17	4	7	15	4	7	13	2	4
March	20	9	12	18	7	9	17	5	9	21	9	12	15	5	7	16	5	8
April	21	9	13	23	11	14	26	15	17	22	11	14	26	14	17	24	13	17
May	27	15	18	31	19	22	29	17	21	29	19	22	30	17	21	28	17	20

[a] Mean, based on the mean hourly temperatures for each month.

and means were separated by Duncan's new multiple range test with $\alpha = 0.05$.

Effects of Temperature on Wetland Nightshade Growth Parameters. This study was conducted to determine growth of wetland nightshade at four temperature regimes. In 1999 and 2000, wetland nightshade plants were established in the greenhouse at Stoneville, MS as described above. Plants were transferred to growth chambers at 1 wk after emergence. Growth chambers were maintained at four temperature regimes of 26/36, 20/30, 14/24, and 8/18 ($\pm$0.5) C night/day with 14 h of daylight. In the growth chambers, lighting was from fluorescent lamps to produce a photosynthetic photon flux density of 200 μmol/m/s. Plant height, node number, and number of leaves were recorded at weekly intervals. Time to first flower (days) was recorded until 11 wk after the wetland nightshade plants were transferred into the growth chambers (12-wk-old plants). Wetland nightshade plants were then clipped at the soil surface, and shoots were oven dried at 45 C for 2 wk and then weighed. All wetland nightshade plants, soil, and pots were autoclaved following each experiment. The experiment was established with main units as a randomized complete block with two blocks and four treatments. Experimental units for main treatments were the growth chambers and were replicated in time, with treatments randomly assigned to growth chambers. Subunits were 11 time intervals and were a repeated measure of subunit. There were eight pots per chamber and the eight pots are subsamples for the main unit treatment and additional level of replication for the time subunit treatments. In analysis of variance, the subunit treatment time was treated as trend. Data were subjected to analysis of variance, and means were separated by Duncan's new multiple range test with $\alpha = 0.05$ and by regression analysis.

Table 2. Percent survival of three wetland nightshade plants transferred into the greenhouse from outdoors each month at Stoneville, MS, from 1996–2002.

	Plant Survival					
Month	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001	2001–2002
November	100	100	100	—	—	—
December	100	100	100	—	—	—
January	100	100	33	—	—	—
February	100	100	33	—	—	—
March	100	0	0	—	—	—
April	0	0	0	—	—	—
May	33	0	33	33	66	33
LSD (0.05)	38	—[1]	66	—	—	—

[1] There is no error term, because all treatments were either 0 or 100.

Wetland Nightshade Winter Survival in Standing Water. This study was conducted to determine the winter survival of wetland nightshade in standing water. Wetland nightshade plants were started in the greenhouse as described above in May of each year (2001 to 2002). Single plants were transplanted into 25-cm-diameter pots and maintained in the greenhouse at temperatures of 20/30 C night/day. In October of each year, three plants in 25-cm-diameter pots were pruned to 10-cm height and transferred outside into a tub of standing water. Water levels were maintained at a depth of 20 cm above the soil level in the pots. Water temperature was recorded when plant sprouting was observed and the time from sprouting until wetland nightshade plants emerged above the water surface level. The experiment was conducted as a completely random design with three (plants) and was repeated the following winter. Data were subjected to analysis of variance, and means were separated by Duncan's new multiple range test with $\alpha = 0.05$.

RESULTS AND DISCUSSION

Wetland Nightshade Winter Survival above Water Level. Wetland nightshade survival was greater than or equal to 33% in 5 of 6 yr (Table 2). The exception was

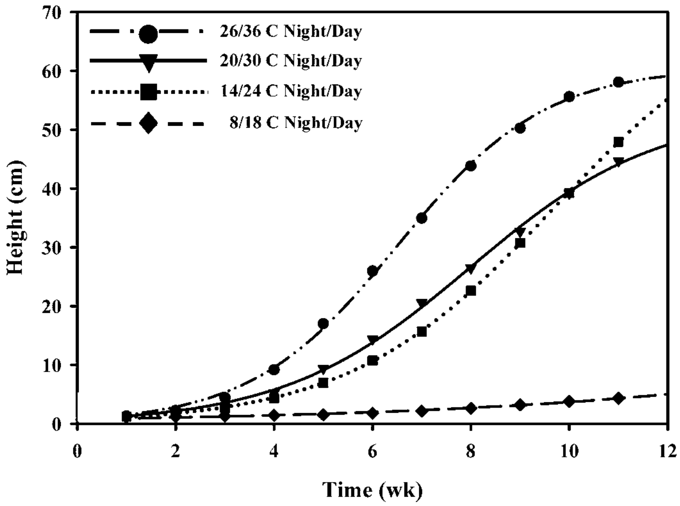

Figure 1. Effects of temperature on wetland nightshade plant height. Regression equations: 26/36 C night/day, $y = 60.65/[1 + \exp(-(x - 6.5)/1.5)]$, $R^2 = 0.99$; 20/30 C night/day, $y = 53.12/[1 + \exp(-(x - 7.99)/1.9)]$, $R^2 = 0.99$; 14/24 C night/day, $y = 73.21/[1 + \exp(-(x - 9.68)/2.07)]$, $R^2 = 0.99$; 8/18 C night/day, $= 243.04/[1 + \exp(-(x - 36.5)/6.35)]$, $R^2 = 0.99$.

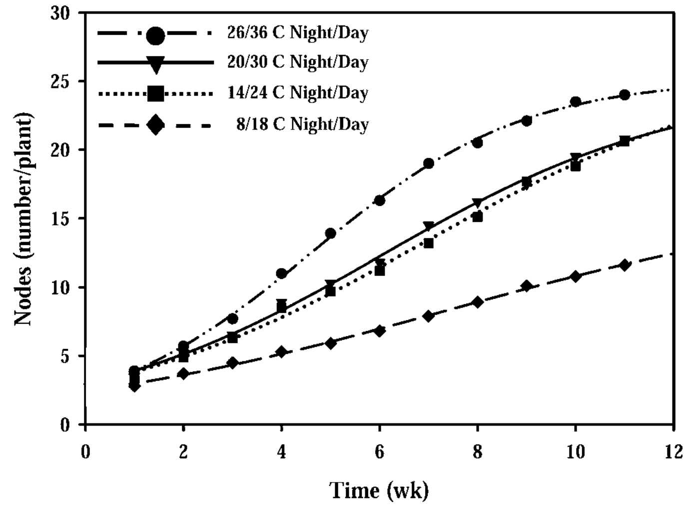

Figure 2. Effects of temperature on wetland nightshade number of nodes/plant. Regression equations: 26/36 C night/day, $y = 25.2/[1 + \exp(-(x - 4.64)/2.15)]$, $R^2 = 0.99$; 20/30 C night/day, $y = 24.68/[1 + \exp(-(x - 6.05)/3.03)]$, $R^2 = 0.99$, 14/24 C night/day, $y = 24.48/[1 + \exp(-(x-6.9)/3.32)]$, $R^2 = 0.99$, 8/18 C night/day, $y = 16.46/[1 + \exp(-(x - 7.29)/4.17)]$, $R^2 = 0.99$.

the winter of 1997 to 1998. Mortality was observed as early as January in 1998 to 1999 compared to 1996 to 1997 or 1998 to 1999 in February and March, respectively. In the years that plants were transferred back into the greenhouse at monthly intervals (first of each month), all wetland nightshade plants survived through December 1 and all wetland nightshade plants survived until March 1 in 1997 and until February 1 in 1998. Wetland nightshade survival was 33% for plants transferred to the greenhouse in February and March of 1999. In the winters of 1996 to 1997, 1997 to 1998, and 1998 to 1999, the numbers of days with maximum and minimum temperatures below freezing were 4, 0, and 8 d, respectively. The period of below 0 C was not over 5 d in 1998 to 1999 (data not shown). Therefore, short-term periods of cold weather (less than or equal to 5 d) were inadequate to cause wetland nightshade mortality (winters of 1996 to 1999) and over a 6-yr period, and average of 33% wetland nightshade plants survived at Stoneville, MS (33°26′). In response to freezing temperatures, the aboveground tissues were killed very quickly. Leaves and stems turned brown and became flaccid, then leaves dropped from plants and stems became brittle. Such wetland nightshade plants appeared dead at the time they were transferred to the greenhouse. Wetland nightshade sprouts originated from roots and greater than 1 cm from the brittle basal stems that were greater than 1 cm in diameter.

The number of days below freezing during the winters that plants remained outside all winter seemed to correspond with temperatures from 1996 to 1999 (Table 1). The 4 C mean temperature during December 1997 was less than the 6 C during December of 1996 and 1998 (Table 1) and may account for the increased mortality during the winter of 1997 to 1998. No periods of less than or equal to 0 C for greater than or equal to 5 d were recorded; however, water in the pots and in the trays holding pots froze completely in January 1997, December 1998, and January 1999. These periods of freezing were longer than plants would have been exposed to in nature because the depth of soil freezing was less than 5 cm for each of these time periods.

Effects of Temperature on Wetland Nightshade Growth Parameters. Because there was no significant ($\alpha = 0.05$) block by treatment interaction, data from the two blocks were combined. From these data, wetland nightshade grew best at night/day temperatures of 26/36 C (Figures 1, 2, and 3; Table 3). Wetland nightshade growth and dry plant weights did not differ significantly at temperature regimes of 20/30 and 14/24 C night/day. Temperatures of 8/18 C night/day significantly reduced wetland nightshade growth and plant weights. At 11 weeks after transfer into the growth chambers (12-wk-old wetland nightshade plants), average wetland nightshade heights were 58, 45, 48, and 4 cm (Figure 1); number of nodes were 24, 21, 21, and 12/plant (Figure 2); numbers of leaves were 62, 31, 36, and 21/plant (Figure 2); plant dry weights were 7.1, 4.9, 5.1, and 0.3 g/plant (Table 3) at temperatures of 26/36, 20/30, 14/24, and 8/18 C night/day, respectively. The average number

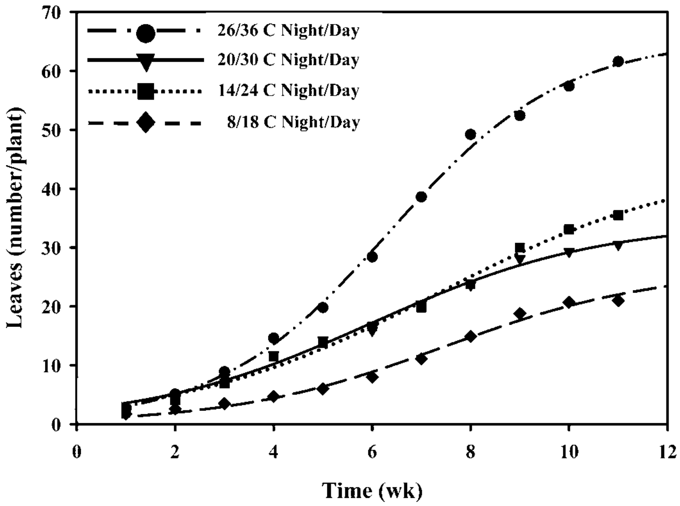

Figure 3. Effects of temperature on wetland nightshade number of leaves/plant. Regression equations: 26/36 C night/day, $y = 65.45/[1 + \exp(-(x - 6.36)/1.76)]$, $R^2 = 0.99$; 20/30 C night/day, $y = 34.34/[1 + \exp(-(x - 5.99)/2.32)]$, $R^2 = 0.99$, 14/24 C night/day, $y = 44.42/[1 + \exp(-(x - 7.34)/2.6)]$, $R^2 = 0.99$, 8/18 C night/day, $y = 26.29/[1 + \exp(-(x - 7.46)/2.16)]$, $R^2 = 0.98$.

of days to flowering was 84, 84, and 79 days after emergence at 14/24, 20/30, and 26/36 C night/day, respectively; however, none of the wetland nightshade plants flowered at 8/18 C (Table 3). Due to the lack of insect pollination, no fruits were produced on wetland nightshade plants under growth chamber conditions.

Wetland nightshade winter survival in standing water. Over the two year period, five of the six (100 and 66% in 2001 and 2002, respectively) wetland nightshade plants sprouted below the water level (data not shown). The water temperature was between 19 and 23 C at first observation of wetland nightshade sprouts. All wetland nightshade plants sprouted from stems rather than lateral to the basal stems as described in the wetland nightshade winter survival above water-level experiment. Wetland nightshade shoots grew above the water surface within 2 to 3 wk. Therefore, wetland nightshade survival of winter conditions can be from plants above the water surface, as in the wetland nightshade winter survival above-water-level experiment, or from below the water surface. In areas where standing water does not freeze for prolonged periods, wetland nightshade survival could be greater than for plants above the water level. Additional research is needed to determine the maximum water depth at which wetland nightshade will survive and the effects of water turbidity at the time of sprouting and emergence of this weed. Likewise, research is needed to determine the minimum temperatures, the length of subfreezing temperatures, and depth of frozen water necessary to cause wetland nightshade mortality.

Table 3. Effects of temperature on wetland nightshade plant weight and days to first bloom at 12 wk after emergence.

Temperature (C) (night/day)	Plant dry weight (g)		Days to first flower
	Stem and leaves	Roots	
8/18	0.3	0.2	None
14/24	5.1	1.5	84
20/30	4.9	1.6	84
26/36	7.1	4.2	79
LSD (0.05)	2.3	0.8	n.s.

Wetland nightshade growth is adequate for flowering and fruit production in other areas of the southeastern United States with summer night/day temperatures at or above 14/24 C, and is compatible with the tropical distribution of this species (Gentry and Standley 1974; Reimus and Robertson 1995; Standley 1924; Wunderlin et al. 1993). Winter temperatures as far north as Stoneville, MS seem to be inadequate for total mortality of established wetland nightshade plants. Based on the present research, wetland nightshade could survive and reproduce in areas farther north in the United States than are currently occupied by this species, suggesting similar results to the potential ecological range for tropical soda-apple (Patterson et al. 1997). These data do not take into account seasonal temperature extremes, precipitation patterns, photoperiods, and depth and turbidity of water on wetland nightshade survival, growth, and reproductive characteristics. However, there are millions of hectares with suitable climatic conditions that equal or exceed 14 hr daylight and equal or exceed 14/24 C night/day temperatures and habitats for wetland nightshade, especially along rivers and streams and around lakes in the southeastern United States. For these reasons, control measures and/or eradication efforts should be continued in Florida to prevent the spread of this pernicious weed into new areas in the southern United States.

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