

Tomato and Nightshade (*Solanum nigrum* L. and *S. ptycanthum* Dun.) Effects on Soil Water Content

Milton E. McGiffen, Jr.¹

Illinois Natural History Survey, Champaign, IL 61820

John B. Masiunas²

Department of Horticulture, University of Illinois, 1201 W. Gregory Drive, Urbana, IL 61801

Morris G. Huck

U.S. Department of Agriculture-Agricultural Research Service, Crop Protection Research Unit, Urbana, IL 61801

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Abstract. Field and greenhouse experiments were conducted to determine the response of eastern black nightshade (*Solanum ptycanthum*), black nightshade (*S. nigrum*), and tomato (*Lycopersicon esculentum* Mill. cv. Heinz 6004) to water stress and the effect of nightshade-tomato competition on soil water content. In the greenhouse, plants were exposed to three water regimes induced by watering either daily, weekly, or biweekly. Water deficit caused a similar decrease in height, weight, and leaf area in all three species. There was more than a 50% reduction in height when the plants were watered biweekly compared with daily watering. Water stress caused a shift in biomass from shoots to roots in all three species. Black nightshade and tomato produced thinner leaves in response to water deficit. Companion field experiments were conducted during the 1989 and 1990 growing seasons in Urbana, Ill. Eastern black nightshade and black nightshade were transplanted at densities of 0.8, 1.6, 3.2, and 4.8 plants/m², 5 days after tomatoes were transplanted. These nightshade densities caused significant reductions in soil water content. In 1989, only the highest density of either nightshade species reduced topsoil water content. In 1990, all densities of nightshade, except the two lowest densities of black nightshade, reduced topsoil water content. Eastern black nightshade consistently had a greater effect on tomato yield than black nightshade. Tomato yields averaged over both years were 17,000 and 8,000 kg·ha⁻¹ at the highest (4.8 plants/m²) density of black and eastern black nightshade, respectively. The decrease in soil moisture from high densities of nightshade could not account for the reduced yields.

Precise water management is critical for successful production of processing tomatoes. Tomato vegetative and fruit growth is very sensitive to water stress (Sanders et al., 1989; Wudiri and Henderson, 1985). Vegetative growth is affected by closure of stomates, leaf rolling, and shifts in assimilate partitioning induced by water stress. When soil water is abundant, the bulk of the assimilated C is partitioned to the shoots, but when water is limiting, roots receive more assimilate (Geddes et al., 1979). The leaves of tomato cultivars such as 'Saladette' roll their leaves under high evaporative demand and thereby escape severe water stress (Wudiri and Henderson, 1985). Rudich et al. (1981) reported that tomatoes close their stomates at a water deficit of -6 bars, reducing water loss and C assimilation at moderate levels of water stress.

Reproduction is generally the most water-stress sensitive of tomato growth stages (Wudiri and Henderson, 1985). Water stress during fruiting affects fruit quality and yield. Adequate soil moisture during flowering, fruit set, and fruit development is critical for maximum tomato yields (Rudich et al., 1977;

Wudiri and Henderson, 1985). Water stress during these growth stages results in fruit failing to develop adequate size (Cannell and Asbell, 1974; Moore et al., 1957; Rudich et al., 1977; Sanders et al., 1989). Excessive moisture during fruit development increases foliar diseases and fruit rots (Geisenberg and Stewart, 1986; Rudich et al., 1977). Tomato fruit quality is improved with moderate water stress because the total and soluble solid concentrations (SSC) are increased (Geisenberg and Stewart, 1986; Mitchell et al., 1991; Rudich et al., 1977; Sanders et al., 1989; Vittum et al., 1961). The increased SSC results from lower water accumulation by the fruit (Mitchell et al., 1991; Vittum et al., 1961).

Water management also affects weed interference. Many weeds can adapt to grow under a wide range of soil moisture conditions (Nadeau and Morrison, 1986). Weed root growth is often rapid, allowing the weeds to exploit soil water reserves held in large soil volumes (Davis et al., 1967). For example, common cocklebur (*Xanthium strumarium* L.) exploits the water reserves held in a large soil volume, thus gaining a competitive advantage over soybean [*Glycine max* (L.) Merr.] (Geddes et al., 1979). But water stress also can shift competition to favor the economic crop. Patterson (1988) reported that water stress reduced spurred anoda [*Anoda cristata* (L.) Schlecht.] and velvetleaf (*Abrutilon theophrasti* Medik.) biomass, thus increasing the competitiveness of cotton.

Eastern black nightshade and black nightshade can significantly reduce tomato yields (McGiffen, 1991; Perez and Masiunas, 1990; Weaver et al., 1987). The critical period for

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¹Current address: Dept. of Botany and Plant Sciences, Univ. of California, Riverside, CA 92521.

²To whom reprint requests should be addressed.

Abbreviation: WAP, weeks after planting.

nightshade interference in tomato is 4 to 8 weeks after crop establishment (Perez and Masiunas, 1990; Weaver, 1984; Weaver and Tan, 1983). This critical phase coincides with the full bloom stage of tomato (Freisen, 1979; Perez and Masiunas, 1990). Tomato yield reduction from nightshade interference is primarily due to shading effects (Weaver and Tan, 1983). If nightshade emerges after tomato, nightshade produces thin shade leaves with less mesophyll (McGiffen et al., 1992). These adaptations increase light use efficiency when nightshades grow under the crop canopy (Stoller and Myers, 1989). The thinner leaves also result in a lower water-use efficiency (Yun and Taylor, 1986). Nightshades compete for the soil moisture available to the crop. Thus, at lower soil water potentials, tomato stomatal conductance and transpiration rates are reduced (Weaver, 1984).

Irrigation schemes for tomatoes have not taken water use from weed interference into account (Al-Jibury and May, 1969; Geisenberg and Stewart, 1986; Rudich et al., 1977; Sanders et al., 1989). Although nightshade interference has a significant impact on tomato yield, we found no literature documenting the effect of that interference on soil water content. Thus, the objective of this study was to determine the relative response of nightshade and tomato to water stress and their effect on soil water content.

Materials and Methods

Effect of water regime on growth (greenhouse experiment). A greenhouse experiment was conducted to characterize the response of eastern black nightshade, black nightshade, and the processing tomato cultivar Heinz 6004 to water regimes. The three species were sown separately in 4-liter pots containing 1 peat : 1 perlite : 1 loam soil (by volume). The seedlings were thinned to one plant per pot 2 weeks after emergence.

Sunlight was supplemented by artificial lighting provided by mercury vapor lamps with an intensity of 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the plant canopy. The photoperiod was 16 h day/8 h night, and the relative humidity was 78% \pm 12%. The greenhouse was at a 24 \pm 3C/18 \pm 2C day/night cycle.

Treatments consisted of three moisture regimes: watering daily, weekly, or biweekly. At each watering, the pots were watered until no further water was absorbed. Water content of the pots ranged from 22% to 70% by weight. The treatments were initiated 3 weeks after emergence, when the plants had two to four true leaves. There were two cycles (2 weeks each) of drought stress. In the first cycle, wilting occurred only in the biweekly treatment. In the second cycle, wilting occurred 5 days after watering. A solution of 0.2 M KNO_3 , 0.02 M KH_2PO_4 , and 0.05 M KCl , resulting in a final concentration ($\mu\text{g}\cdot\text{ml}^{-1}$) of 210 N, 31 P, and 234 K was applied every 2nd week to all treatments. The experiment was a randomized complete block with four replications and was repeated.

Plants were harvested 7 weeks after emergence. Shoot height was measured just before harvest of fruit. After harvest, the plants were divided into leaf, stem, and root tissue. Leaf area was determined using a LI-COR 3100 leaf area meter (LI-COR, Lincoln, Neb.). Dry weights of leaves, stems, and roots were determined by drying the tissue for 5 days at 70C. Specific leaf area, an indicator of leaf thickness, was determined by dividing leaf area by leaf weight.

Effect of nightshades on soil water content, photosynthesis, and yield (field experiment). Five-week-old 'Heinz 6004' processing tomato transplants were planted in Urbana, Ill., on 23 May 1989 and 18 May 1990. The site is flat, with minimal slope. Plots were 2.7 \times 5.7 m and included three rows of 12

tomato plants each. Tomato spacing was 45 cm within the row and 90 cm between rows. The soil type was a Flanagan silt loam (fine montmorillonitic, mesic, Aquic Argiudoll) with 4% to 5% organic matter and a pH of 6.2. The field capacity was 41% and wilting point 13% (J. Wang and M.G. Huck, unpublished data). Urea was applied at a rate of 240 $\text{kg}\cdot\text{ha}^{-1}$ before both seasons. Trifluralin at 0.8 kg a.i./ha was incorporated into the soil before planting to control weeds other than nightshade. After tomatoes were established, weeds that emerged were removed by hand.

There were nine tomato-nightshade intercrop treatments, consisting of a control (tomatoes with no nightshade) and either black or eastern black nightshade planted into the tomato rows at densities of 0.8, 1.6, 3.2, or 4.8 nightshade plants/m². Nightshades were established as two-leaf transplants when tomatoes had recovered from transplanting (5 days after tomatoes were planted). The experiment was a randomized complete block with five replications.

Neutron probe access tubes were installed immediately after incorporation of trifluralin and before planting of tomatoes. As the access tubes were installed, soil core samples were removed at 15-cm increments to a depth of 150 cm to allow gravimetric determination of soil water content. Initial neutron probe measurements were recorded as the tubes were installed to allow calibration against gravimetric water content values determined from the core samples. Additional gravimetric samples from 15-cm increments to a depth of 150 cm were taken during the 2nd week of July, after significant drying of subsurface horizons had occurred.

Throughout both growing seasons, neutron probe readings were taken at 30-cm increments down to 150 cm below the soil surface. The neutron probe readings were taken immediately before or 3 days after each rainfall or irrigation. Rainfall was supplemented with sprinkler irrigation to provide an average of 25 mm water/week, according to standard practices (Lorenz and Maynard, 1980). There was no wilting of tomato or nightshade plants. No irrigation or rainfall occurred during the 7th or 10th weeks after planting (WAP) in either year (Table 1). The total amount of water depleted from the soil each year was determined as the difference between the maximum and minimum soil water content readings.

To determine if eastern black nightshade, black nightshade, or tomato differed in their physiological responses to moisture

Table 1. Weekly rainfall and irrigation at Urbana, Ill., during the 1989 and 1990 growing seasons.

WAP	1989 (mm)	1990 (mm)
1	59	30
2	24	6
3	3	50
4	40* ^z	32
5	98	80
6	4	43
7	0	0
8	40*	52
9	41	29
10	0	0
11	40*	40*
12	0	19
13	2	0
Total	351	381

^zDenotes 40 mm water applied using sprinkler irrigation.

stress, photosynthetic rate and stomatal conductance were measured weekly from the 4th through the 11th WAP. Measurements were taken at 1100-1300 HR solar time on clear days when solar irradiance at the leaf level was $> 1600 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Recently fully expanded leaves of each species were measured in situ with a LI-COR 6200 closed portable photosynthesis system with a 4-liter chamber. Two readings per species were taken from plants in the center row of each plot, and the data were averaged.

During week 13, tomato fruits were harvested by hand from the center row of each plot and weighed. More than 60% of the tomatoes in the control plots were at the pink stage of ripeness (Manley, 1983) when harvested. A random sample of 50 fruits from each plot was weighed to determine individual fruit weight. The sample was then graded according to U.S. Dept. of Agriculture (USDA) standards (Manley, 1983), and the percentages of USDA no. 1, green, and rotted tomatoes were determined.

Data from both experiments were tested using analysis of variance. Interactions with repeats (greenhouse) or years (field) were determined, and where possible data were combined. When significant treatment differences occurred, the means were separated using the least significant difference procedure. Photosynthetic and yield data were subjected to regression analysis.

Results and Discussion

Effect of water regime on growth (greenhouse requirement). Eastern black nightshade, black nightshade, and tomato responded similarly to water stress. A decrease in watering frequency decreased the dry weight, height, and leaf area of all three species (Table 2). Across all watering regimes, black nightshade was the tallest, had the largest leaf area, and was the heaviest of the three species. When watered daily, mean heights were 53, 34, and 38.5 cm for black nightshade, eastern black nightshade, and tomato, respec-

Table 2. Effect of watering frequency on the height, biomass, and leaf area of black nightshade, eastern black nightshade, and tomato in the greenhouse experiment. Results are the average of two experiments.

Plant characteristic	Watering frequency			LSD _{0.05}
	Daily	Weekly	Biweekly	
Ht (cm)				
Black nightshade	53.3	36.0	22.8	4.5
Eastern black	34.0	23.0	14.8	2.9
Tomato	38.5	24.5	18.9	2.6
Leaf wt (g)				
Black nightshade	6.55	3.83	1.93	0.42
Eastern black	5.25	4.03	1.80	0.60
Tomato	6.30	3.52	1.52	0.83
Stem wt (g)				
Black nightshade	4.85	2.15	1.03	0.51
Eastern black	3.18	2.22	0.82	0.37
Tomato	4.58	1.95	0.78	0.59
Root wt (g)				
Black nightshade	3.20	2.18	1.30	0.72
Eastern black	1.65	1.00	1.00	0.64
Tomato	2.45	1.68	1.02	0.29
Leaf area (cm ²)				
Black nightshade	1530	910	615	128
Eastern black	1800	1210	593	119
Tomato	1330	888	398	227
Specific leaf area (cm ² ·g ⁻¹)				
Black nightshade	234	238	320	19.4
Eastern black	344	300	330	28.8
Tomato	211	252	260	26.0

tively. When watered biweekly, there was $>50\%$ reduction in height for all three species.

Water regime also affected biomass production. Total biomass production for black nightshade watered daily was 14.6 g but only 4.25 g when watered biweekly. There was no effect of water regime on the portion of biomass allocated to leaves. All three species increased the percentage of biomass in the roots as watering frequency decreased. Averaged over all three species, when the plants were watered daily, 20% of the biomass was allocated to roots; 30% of the biomass was allocated to the roots when the plants were watered biweekly.

Across all watering regimes, tomatoes had the least and black nightshade had the most leaf area per unit land area. In each species, leaf area decreased as the water deficit increased. Specific leaf area of black nightshade and tomato increased as the frequency of watering decreased. This result indicates that black nightshade and tomatoes responded to a reduction in watering frequency by growing thinner leaves, in contrast to the increased leaf thickness reported for species adapted to water stress (Yun and Taylor, 1986). We observed no increase in the specific leaf area of eastern black nightshade as the frequency of watering decreased.

Effect of nightshades on soil water content, photosynthesis, and yield field experiment). The overall amount of moisture supplied to the crop was similar in both years (Table 1). Less rainfall fell during Summer 1989 than in 1990; thus, irrigation was required during 3 weeks of the 1989 growing season but only during 1 week of the 1990 season. Forty-five percent of the total volume of water added to the soil during the 1989 growing season came from irrigation, but only 10% of the water needed to replace losses came from irrigation in 1990. About 60% of the total was added during the first 7 weeks of the growing season each year, before tomato flowering began. Soil water content of the upper and lower strata declined from 5 WAP through harvest (12 WAP in 1989, 11 WAP in 1990); when measured, soil water content was lower than at any time during the growing season (Fig. 1).

The heaviest rainfall (wettest week of the growing season) occurred 5 WAP in both 1989 and 1990 (Table 1). There was a substantial increase in soil water content at 5 WAP in 1989 for both the topsoil (0 to 60 cm, Fig. 1) and the subsoil (60- to 150-cm soil depths, Fig. 2), indicating that a large portion of the 98 mm of rain that fell that week had percolated downward through the soil profile. Because this rain fell as several showers instead of a single rainfall event, runoff was minimal. However, during the 1990 growing season, most of the rain that fell 5 WAP was in a single event lasting <4 h, which saturated the soil surface before moisture could percolate down into the deeper soil layers. Although not measured in 1989 or 1990, runoff was only observed during this rainfall event.

Nightshade competition influenced topsoil water content (Fig. 1). In 1989, the first significant differences in topsoil water content between treatments occurred 9 WAP, while in 1990, the first differences were at 6 WAP, since the season began with significantly lower subsoil water reserves (Fig. 2). Nightshade density did not cause a significant difference in subsoil water content (< 60 cm) in either year.

The treatments that caused significant reductions in topsoil water content also differed between years. In 1989, significant differences in soil water content resulted from variation in weed density, regardless of whether the species was black or eastern black nightshade. In 1990, the lower density (1.6 plants/m²) of black nightshade had no effect on topsoil water content (com-

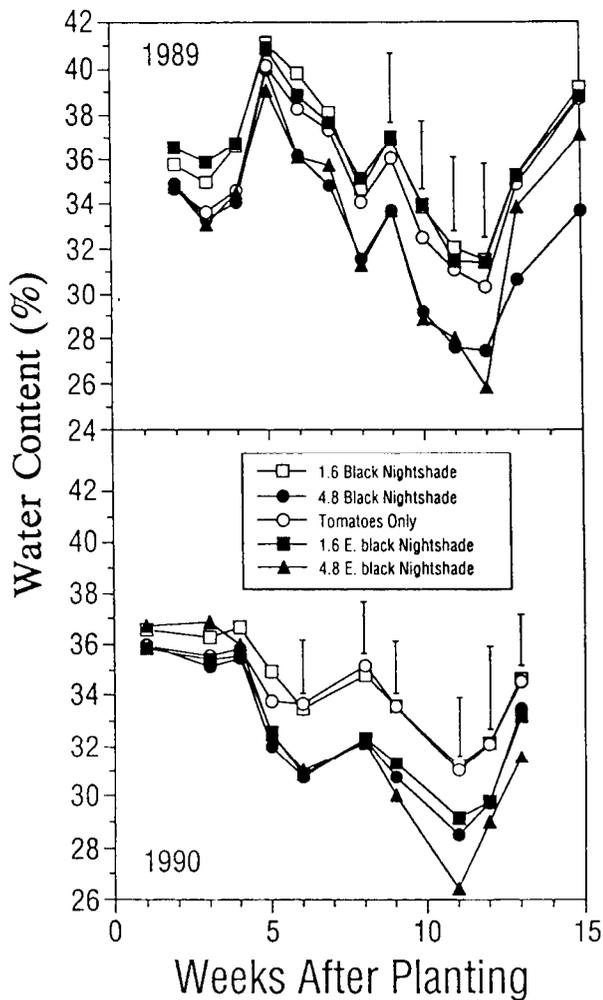


Fig. 1. Water content (percent by volume) of topsoil (upper 60 cm) of tomato plots with various nightshade densities. The vertical bars represent confidence limits with a significance of $P \leq 0.05$. Time points without bars did not have significant differences in soil water content between treatments. Top, 1989, bottom, 1990 growing seasons.

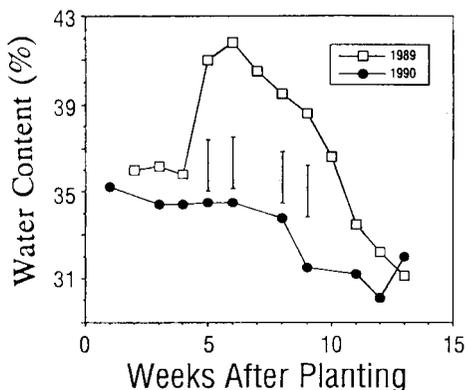


Fig. 2. Mean water content (percent by volume) of subsoil (60-150-cm depth). There was no effect of nightshade density on subsoil water content. The vertical bars represent confidence limits with a significance of $P \leq 0.05$. Time points without bars were not significantly different.

pared with weed-free control plots). Compared with the weed-free control, soil water content was lower in the highest density

of both nightshade species through the mature green stage of tomatoes (10 WAP), and for 4.8 eastern black nightshade plants/ m^2 through 13 WAP.

Due to a higher initial soil water content, nearly twice as much water was depleted from the profile in 1989 as in 1990 (data not shown). Soil water extraction patterns are indicative of rooting depth and distribution (Ristaino and Duniway, 1991; Taylor and Klepper, 1976), so more roots may have been concentrated in the upper 60 cm of the profile in 1990 than in 1989. The possible higher concentration of roots in a smaller volume of soil during 1990 may explain why nightshade competition caused a decline in tomato quality and number of green fruits in 1990 but not in 1989. Cannel and Asbel (1974) also found that late-season declines in soil water content resulted in fewer green fruit but had no effect on marketable yield.

Photosynthetic rate was related to stomatal conductance (Fig. 3). Black nightshade responded to increased stomatal conductance by assimilating C more quickly than either tomato or eastern black nightshade. Photosynthetic rates for eastern black nightshade and tomato were relatively insensitive to changes in stomatal conductance. Tomato photosynthetic rates ranged from 10 to 40 $\mu\text{mol CO}_2/\text{sec per m}^2$. The range of photosynthetic rates for tomato was less than the range measured for black nightshade but was similar to those of eastern black nightshade.

Black nightshade density did not affect total tomato yield (USDA no. 1 and greens) in 1989. Eastern black nightshade and black nightshade decreased total yield (Fig. 4). In both years, yield declined linearly with eastern black nightshade density. Eastern black nightshade consistently had a greater effect on yield than black nightshade. For example, in 1989, 19,000 and 9000 kg fruit/ha were harvested in plots containing 4.8 plants/ m^2 of black or eastern black nightshade, respectively.

In 1989, nightshade density did not have a significant effect on tomato grades. But in 1990, black or eastern black nightshade density affected fruit quality, increasing the percentage of USDA no. 1 fruit (Fig. 5). However, eastern black nightshade consistently resulted in more green tomato fruit than black nightshade.

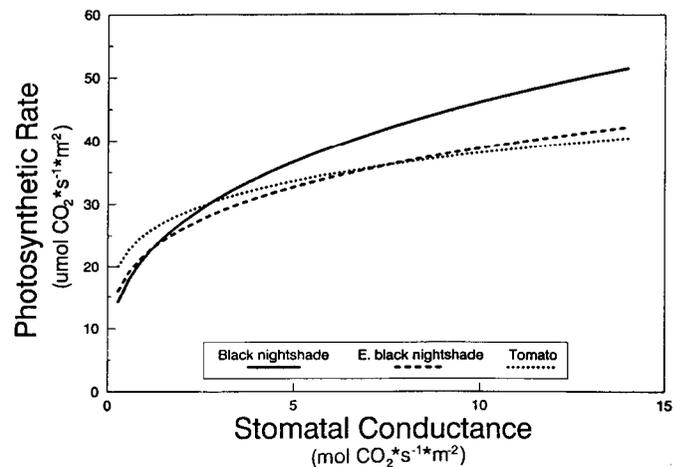


Fig. 3. Relation between stomatal conductance and CO_2 fixation rate of black nightshade, eastern black nightshade, or tomato. Each equation is the result of > 100 data points from the combined 1989 and 1990 results. The regression equations are: black nightshade, Photosynthetic rate = 21.5 (Stomatal Conductance) $^{0.33}$, $r^2 = 0.54$; eastern black nightshade, Photosynthetic rate = 21.9 (Stomatal Conductance) $^{0.25}$, $r^2 = 0.39$; and tomato, Photosynthetic rate = 25.08 (Stomatal conductance) $^{0.17}$, $r^2 = 0.32$. The equations were significant at $P \leq 0.05$.

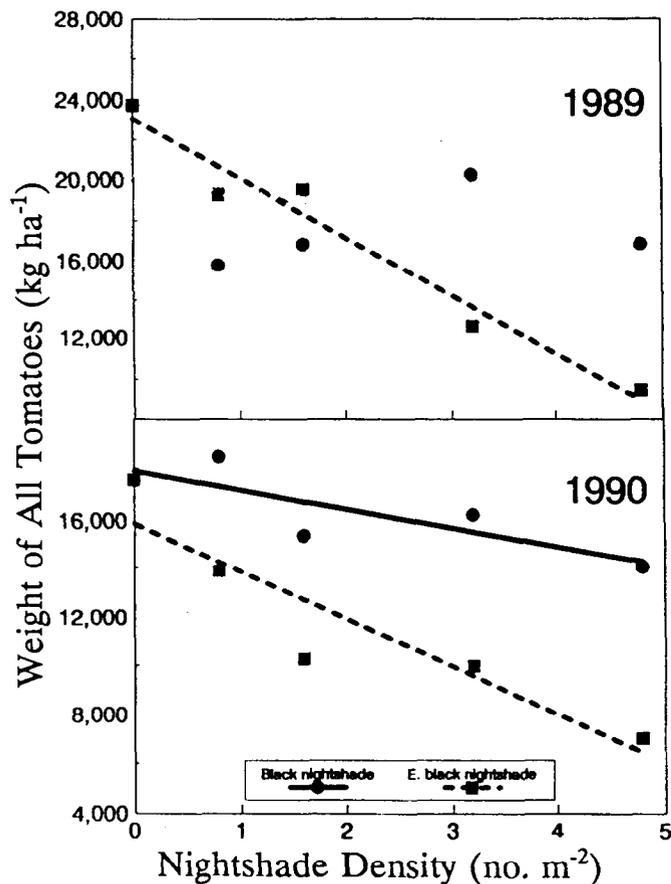


Fig. 4. Total weight of all classes of tomatoes (including USDA no. 1, greens, and rotten) as a function of nightshade density. The regression equations are for 1989: black nightshade, no significant regression; eastern black nightshade, $Yield = 23,000 - 2,930 (\text{no./m}^2)$, $r^2 = 0.96$. In 1990, the regression equations are: black nightshade, $Yield = 17,800 - 758 (\text{no./m}^2)$, $r^2 = 0.69$; eastern black nightshade, $Yield = 15,800 - 1,950 (\text{no./m}^2)$, $r^2 = 0.86$. The equations were significant at $P \leq 0.05$.

The decrease in soil moisture from high densities of nightshade caused no measurable water stress in tomatoes. Tomato stomatal conductance was the same across all treatments, and there were no treatment effects on water content in the deeper soil profiles (60 to 1.50 cm). Further, although the effect of eastern black nightshade on soil water content was equivalent to the effect of the highest density of black nightshade, only eastern black nightshade decreased tomato yield in both years.

We therefore conclude that the primary cause of tomato yield loss from weed interference is shading (Friesen, 1979; McGiffen, 1991; Weaver and Tan, 1983). Eastern black nightshade shades tomatoes for more of the critical reproductive stage than does black nightshade (McGiffen, 1991). Eastern black nightshade also is better adapted to compete for light because its specific leaf area increases more rapidly than that of black nightshade (McGiffen, 1991), thus increasing photosynthetic efficiency when shaded. Our results did not show significant competition of nightshades with tomatoes for water.

The tomato growth stage during which soil moisture is reduced from weed interference may be important in determining the impact of competition for moisture on crop yield. Soybeans are most vulnerable to competition with velvetleaf early in the season, before the crop's root system has fully developed (Munger et al., 1987). Late-season water stress caused three times

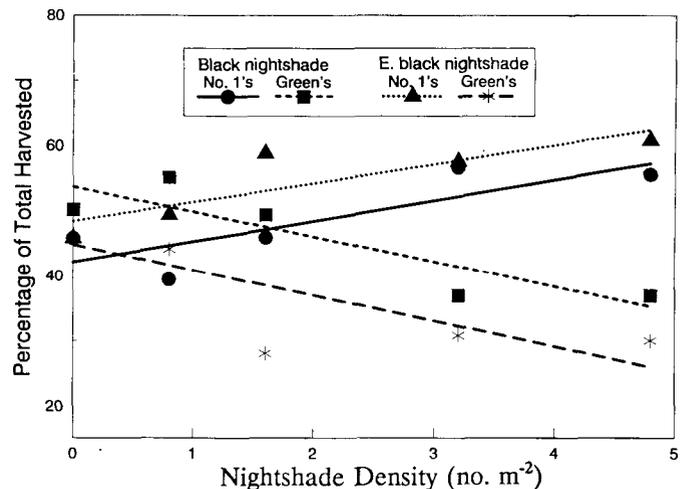


Fig. 5. Effect of nightshade density on the percentage of tomatoes graded as USDA no. 1 or green. Only 1990 data are presented, because in 1989, nightshade density did not have a significant ($P \leq 0.05$) effect on grades. The regression equations are: 1) the effect of black nightshade on percent no. 1's, $Y = 42.1 + 3.17 (\text{no./m}^2)$, $r^2 = 0.69$; 2) the effect of black nightshade on percent green, $Y = 53.7 - 3.84 (\text{no./m}^2)$, $r^2 = 0.79$; 3) the effect of eastern black nightshade on percent no. 1's, $Y = 48.4 + 2.91 (\text{no./m}^2)$, $r^2 = 0.74$; and 4) the effect of eastern black nightshade on percent green, $Y = 44.8 - 3.92 (\text{no./m}^2)$, $r^2 = 0.58$.

as much yield loss from yellow foxtail competition with soybeans than when drought occurred at other times in the growing season (Nadeau and Morrison, 1986). In our study, reductions in soil moisture from nightshade interference occurred after flowering, with the largest differences observed after the mature-green stage. Most of the yield in processing tomatoes is derived from pollination during the first 15 days of flowering (Rudich et al., 1977). This period precedes the time nightshade reduced soil moisture in our study.

Modifications in cultural practices may reduce or eliminate competition for soil moisture. Transplanting, for example, gives tomatoes an initial size advantage over the nightshade. Initial size of the co-occurring species is an important determinant of competition (Alm et al., 1991). The initial size advantage of tomatoes may have delayed the onset of differences in soil water content due to the treatments until late in the season, after much of the yield is determined. The use of trickle irrigation and plastic mulches could also affect the ability of weeds to compete for soil moisture.

Reductions in soil water content from weed interference may be important when light does not limit tomato growth. Transplanted tomatoes in the reproductive stage of growth have 85% of their roots in the upper 30 cm of the soil (Portas and Dordio, 1980), where reductions in soil water content from nightshade interference occur. This could make tomatoes extremely sensitive to competition for moisture. The potential susceptibility may be overcome by developing tomato cultivars that maximize water-use efficiency, produce dense canopies, and develop root systems rapidly.

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