Path Analysis of Tomato Yield Components in Relation to Competition with Black and Eastern Black Nightshade

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Abstract. Path analysis is a statistical method for determining the magnitude and direction of multiple effects on a complex process. We used path analysis to assess 1) the impact of black nightshade (*Solanum nigrum* L.) or eastern black nightshade (*Solanum pycnanthum* Dun.) competition on the yield components of 'Heinz 6004' processing tomato (*Lycopersicon esculentum* Mill.) and 2) the relationship between tomato yield components and total and marketable yield. Either black or eastern black nightshade was interplanted with tomatoes at population densities from 0 to 4.8/m². Path analysis revealed that increasing weed population density led directly to fewer green and total fruit per plant, two components of marketable yield. However, the percentage of culls per plant and fruit weight were not affected by nightshade population density. Using correlation coefficients alone would have led to the erroneous conclusion that the percentage of culls did not affect marketable yield; our path analysis demonstrated that decreasing the percentage of culls through breeding or cultural practices will strongly affect marketable yield. The total number of fruit was the most important yield component in determining total and marketable yields per plant. Breeding and management practices that maximize fruit set, increase maturity at harvest, and decrease the percentage of culls would be expected to increase marketable yield.

Nightshade interference affects yield by limiting the resources (i.e., light, water, and nutrients) available to the crop. In general, competition for resources does not reduce crop stand, but reduces marketable yield by affecting the number, weight, or quality of tomatoes (Lange et al., 1986; McGiffen et al., 1992a; Perez and Masiunas, 1990; Weaver and Tan, 1987). Nightshade interference decreases the number of fruit, but not the average fruit weight (Maillet and Abdul-Fatah, 1983).

The effect of nightshade competition on tomato yield is determined largely by the weight and phenological stage of the crop when competition occurs. Since field-seeded tomatoes do not have the initial size advantage of transplants, they are more likely to be shaded by nightshade (Weaver and Tan, 1987). Directly seeded tomato plants, therefore, are affected more severely by weed competition than transplanted tomatoes (Weaver et al., 1987). If eastern black nightshade is not present during tomato full bloom, transplant yield is unaffected (Perez and Masiunas, 1990). Competition for light imposed by either black or eastern black nightshade during flower and fruit initiation decreases yield largely by decreasing the number of tomatoes per plant (McGiffen et al., 1992a). During tomato reproductive growth, only eastern black nightshade (not black nightshade) shades the canopy severely enough to result in economically significant yield loss (McGiffen et al., 1992a).

Weed competition also may affect fruit quality and the number of marketable fruit. Nightshade competition may reduce marketability by inducing blossom-end rot, a common disorder of tomatoes (Perez and Masiunas, 1990). In abnormally wet years, nightshade competition can increase overall crop quality by decreasing the proportion of fruit graded as green (McGiffen et al., 1992b). Competition does not affect fruit color, soluble solids concentration, acidity, or juice sugar content (Damato and Montemurro, 1986; Friesen, 1979; Monaco et al., 1981).

Path analysis helps determine the importance of the cause and effect relationships between weed population density and crop yield (Pantone et al., 1989). Hypothesized systems of causal relationships between yield components and yield can be tested using path analysis (Dewey and Lu, 1959; Duarte and Adams, 1972; Hancock et al., 1984). For example, Pantone et al. (1992) determined that weed competition had a negative effect on the number of cultivated rice panicles and florets per panicle but had little effect on grain weight. Path analysis showed that biocontrol agents for fiddleneck (*Amsinckia intermedia* Fischer & Meyer) would be more effective if they decreased the number of inflorescences per plant rather than the number of flowers per inflorescence, seeds per flower, or biomass per seed (Pantone et al., 1989).

Path analysis determines the significance of correlations between yield components and assigns a relative importance to yield components or yield relationships. The variables may be related either directly or indirectly. If the variables are indirectly related, path analysis elucidates how other variables mediate the relationships. Consequently, effects that are additive (reinforce each other) or subtractive (cancel each other) may be identified. For example, simple correlations may indicate that the percentage of culls has no effect on yield. However, the correlation coefficient may have resulted from combined effects that indirectly affect

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culls in opposite directions; e.g., a strongly positive increase in yield from total number of fruit and a negative effect from percentage of green fruit that combine for a net effect of zero. Path coefficients for the indirect effects of total and green fruit counts on yield via percentage of culls would be positive and negative, respectively, thus indicating that they increase or decrease yield.

The coefficients generated by path analysis are standardized partial regression coefficients (Afifi and Clark, 1984; Karlsson et al., 1988; Li, 1975; Loehlin, 1987; Puri et al., 1982; Ranalli et al., 1981). Path coefficients are scaled in terms of standard deviations so that the direct and indirect effects associated with different yield components and yield can be compared (Wright, 1921, 1934). Thus, the path coefficients for yield components, such as percentage of green fruit or culls, may be compared to determine the importance of these effects compared to other yield components. This type of analysis is especially important in breeding or management programs that can enhance some yield components but may also result in undesirable changes in others.

The objectives of this study were to quantify the effects of black and eastern black nightshade competition on processing tomato yield components and to elucidate the relationships between yield components and yield. We expected that path analysis would help determine whether reductions in marketable yield from nightshade competition were due to fewer tomatoes, smaller fruit, or reduced fruit quality.

Materials and Methods

Five-week-old 'Heinz 6004' processing tomatoes were transplanted at Urbana, Ill., on 23 and 18 May 1989 and 1990, respectively. Plots were 2.7×5.7 m and included three rows of 12 tomato plants each. There was 0.46 m between each plant within the row, and the rows were 0.9 m apart. 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. To simulate nightshade populations that remain after cultivation, two-leaf black or eastern black nightshade plants 5 cm tall were transplanted into the tomato row 5 days after the crop was transplanted.

The experiment was a randomized complete-block design with five replications. There were nine treatments, including a control (no weeds) and either black or eastern black nightshade at 0.8, 1.6, 3.2, and 4.8 plants/m². Rainfall was supplemented with overhead

sprinkler irrigation to provide at least 25 mm of water per week. 2,6-Dinitro-N,N-dipropyl-4-(trifluoromethyl)benzenamine (trifluralin) at 0.84 kg·ha⁻¹ was applied preplant and incorporated to control weeds other than the two nightshade species.

All tomatoes from the 12 plants in the center row of each plot were harvested by hand 13 weeks after transplanting. More than 60% of the tomatoes in the control plots were past the pink ripeness stage. After total fruit weight was determined, a random sample of 50 fruit from each plot was weighed to determine individual fruit weight. The sample was graded according to U.S. Dept. of Agriculture (USDA) standards (Manley, 1983) and the number of marketable fruit (U.S. no. 1), green fruit, and culls was determined. Culls were rejected for market for reasons other than immaturity; e.g., rotted fruit.

When the tomatoes were harvested, the central two tomato plants and two nightshade plants from the middle row of each plot were cut at the soil line and dry weights were determined. Tomato shoot (without fruit) dry weights ranged from 50 g/plant when no nightshade plants were present to 20 g/plant when 4.8 eastern black nightshade plants/m² were present. Having 4.8 black nightshade/m² resulted in a tomato shoot weight of 36 g/plant. Eastern black nightshade shoot weight ranged from 220 g/plant (with berries) with 0.8 plants/m² to 130 g/plant with 4.8 plants/m². Black nightshade shoot dry weight was 80 g/plant at all population densities. McGiffen et al. (1992a) discussed in detail the effects of nightshade population density on tomato and nightshade biomass production and partitioning.

A general linear model analysis indicated that there was no significant treatment $\times$ year interaction for yield or any of its components. Therefore, results from the 2 years were combined (Neter and Wasserman, 1974; Steel and Torrie, 1980) for the path analysis.

Eight variables were used to prepare a path analysis: 1) eastern black nightshade population density (plants/m²); 2) black nightshade population density (plants/m²); 3) green fruit (number/plant); 4) culls (number/plant); 5) total fruit (number/plant); 6) fruit weight (g/fruit); 7) total tomato yield (kg/plant); and 8) yield of marketable tomatoes (kg/plant). We partitioned total and marketable yields into the following components: percentage of green fruit and culls, total number of fruit, and fruit weight. Because the direct and indirect effects were partitions of the simple correlation coefficients, the sum of the direct and indirect effects equaled the

Fig. 1. Path diagram for the relationships between eastern black and black nightshade densities (variables 1 and 2), yield components of tomato (variables 3-6), and total and marketable tomato yields per plant (variables 7 and 8). Single-headed arrows represent the direct effects that are measured by path coefficients (P_{ij}), and the double-headed arrows depict simple correlations (r_{ij}). *, ** Significant at $P \leq 0.05$ or 0.01, respectively. All other direct effects or simple correlations were nonsignificant.

correlation between individual yield components and total or marketable yield per plant.

We hypothesized the causal relationships shown in Fig. 1. As the relationship between low nightshade densities and tomato yield is linear (McGiffen et al., 1992b), multiple linear regression (Draper and Smith, 1981; SAS Institute, 1985) was used to calculate the path coefficients and correlation coefficients. When no correlation existed between the predictor (independent) variables, the path coefficient was equal to the simple correlation between the predictor and criterion (dependent) variable (Sokal and Rohlf, 1981). This occurred for the paths from the nightshade densities to the yield components.

Simple correlations were hypothesized between yield components. The correlation coefficients are numbers next to the lines with two-headed arrows in the path-analysis diagram (Fig. 1). Black and eastern black nightshade population densities were independently selected variables and, thus, were uncorrelated ($r = 0$). Path coefficients, indicated by single-headed arrows in the path-analysis diagram (Fig. 1), measured the direct effects of one variable on the other. Direct comparisons between corresponding path coefficients were possible because the path coefficients were standardized partial regression coefficients and, thus, were on the same scale.

When independent variables in regression models are correlated, collinearity may result in errors in the estimated regression parameters (McGiffen et al., 1988). We determined that collinearity was not a problem for any of the regressions that make up our path analysis. Condition indexes were <30 and variance decomposition and inflation factors were also low, a response indicating that collinearity did not affect parameter estimates (Belsley et al., 1980).

We tested path analyses other than the one presented in Fig. 1. However, correlations among the independent variables were high and collinearity was a problem. Further, this analysis follows the same format as previous path analyses on population density–yield relationships (Pantone et al., 1989, 1992).

The normal equations for the relationships hypothesized between the yield components and total yield in Fig. 1 are

$$r_{37} = P_{37} + r_{34}P_{47} + r_{35}P_{57} + r_{36}P_{67} \quad [1]$$

$$r_{47} = r_{34}P_{37} + P_{47} + r_{45}P_{57} + r_{46}P_{67} \quad [2]$$

$$r_{57} = r_{35}P_{37} + r_{45}P_{47} + P_{57} + r_{56}P_{67} \quad [3]$$

$$r_{67} = r_{36}P_{37} + r_{46}P_{47} + r_{56}P_{57} + P_{67} \quad [4]$$

The normal equations hypothesized for the path analysis of marketable yield (8) were

$$r_{38} = P_{38} + r_{34}P_{48} + r_{35}P_{58} + r_{36}P_{68} \quad [5]$$

$$r_{48} = r_{34}P_{38} + P_{48} + r_{45}P_{58} + r_{46}P_{68} \quad [6]$$

$$r_{58} = r_{35}P_{38} + r_{45}P_{48} + P_{58} + r_{56}P_{68} \quad [7]$$

$$r_{68} = r_{36}P_{38} + r_{46}P_{48} + r_{56}P_{58} + P_{68} \quad [8]$$

P_{ij} represents path coefficients and r_{ij} represents simple correlation coefficients. Each normal equation partitions the simple correlation coefficient into the direct effect (measured by the path coefficient) and indirect effects (measured by correlation coefficients) via correlated yield components. The subscripts used in the

normal equations, Tables 1–3, and Fig. 1 represent variables included in the path; e.g., P_{37} is the direct effect of percentage of green fruit (subscript 3) on total yield (subscript 7).

The effects of black and eastern black nightshade population density on total and marketable yields were measured with compound paths. Compound paths were calculated from the product of the constituent paths for each yield component (Sokal and Rohlf, 1981).

The steps in deriving the path coefficients are summarized as follows:

- 1) A multiple regression was performed using the population densities of black and eastern black nightshade as independent variables, and a yield component such as percentage of green fruit as the dependent variable.
- 2) This was repeated for each yield component.
- 3) Percentage of green fruit and culls, total number of fruit, and fruit weight were used as independent variables in a multiple regression of total yield.
- 4) Percentage of green fruit and culls, total number of fruit, and fruit weight were used as independent variables in a multiple regression on marketable yield.
- 5) The standardized partial regression coefficients from each of the regressions in steps 1–4 were used as the path coefficients (numbers on the single-headed arrows) in Fig. 1.
- 6) The values for the double-headed arrows were the simple correlations between yield components.
- 7) The indirect effects were determined by multiplying the simple correlations (double-headed arrows) by the path coefficients (single-headed arrows); e.g., the indirect effect of percentage of green fruit on total yield via percentage of culls (Table 1).
- 8) Compound paths were calculated by multiplying path coefficients; e.g., the effect of eastern black nightshade population density on total yield via percentage of green fruit is $-0.31 \times 0.01 = -0.0031$; i.e., 0.0 (Table 3).

Results and Discussion

The only yield components that responded to nightshade population density were the percentage of green fruit and total number of fruit (Fig. 1). The path coefficients for the direct effects of eastern black nightshade were -0.31 and -0.78 , on the percentage of green fruit and total number of fruit, respectively. The effects of black nightshade on the percentage of green fruit and total number of fruit were weaker (-0.28 and -0.42). The responses of percentage of culls and fruit weight to weed population density were not significant, a result indicating that density-independent effects were more important in determining their variation.

Several yield components were correlated (Fig. 1). An increase in the total number of fruit was associated with an increase in the percentage of green fruit ($r_{35} = 0.32$). An increased percentage of green fruit was associated with a decreased percentage of culls [$r_{34} = (-0.65)$]. Greater fruit weight was positively correlated with percentage of culls ($r_{46} = 0.21$).

The only yield components correlated with total yield per plant

Table 1. Path analysis of the effects of the yield components on total yield of tomatoes (kg/plant). Significance levels are presented for the coefficients of determination, direct effects, and simple correlations only.^z

Pathway	Coefficient
Green fruit (%) vs. total yield	
Direct effect, P_{37}	0.01
Indirect effect via culls (%), $r_{34}P_{47}$	-0.05
Indirect effect via total fruit (no.), $r_{35}P_{57}$	0.28
Indirect effect via fruit weight, $r_{36}P_{67}$	-0.08
Total correlation, r_{37}	0.16
Culls (%) vs. total yield	
Direct effect, P_{47}	0.07*
Indirect effect via green fruit (%), $r_{34}P_{37}$	-0.01
Indirect effect via total fruit (no.), $r_{45}P_{57}$	-0.02
Indirect effect via fruit weight, $r_{46}P_{67}$	0.10
Total correlation, r_{47}	0.14
Total fruit (no.) vs. total yield	
Direct effect, P_{57}	0.87**
Indirect effect via green fruit (%), $r_{35}P_{37}$	0.00
Indirect effect via culls (%), $r_{45}P_{47}$	0.00
Indirect effect via fruit weight, $r_{56}P_{67}$	0.00
Total correlation, r_{57}	0.87**
Fruit weight vs. total yield	
Direct effect, P_{67}	0.46**
Indirect effect via green fruit (%), $r_{36}P_{37}$	0.00
Indirect effect via culls (%), $r_{46}P_{47}$	0.01
Indirect effect via total fruit (no.), $r_{56}P_{57}$	-0.01
Total correlation, r_{67}	0.46**
Coefficient of determination (R^2)	0.98**
Residual, U	0.14

^zThe normal equations for the relationships are in the general form $r_{ij} = P_{ij} + \sum w_k r_{ki} P_{kj}$.

***Significant at $P \leq 0.05$ or 0.01, respectively. All other direct effects or simple correlations were nonsignificant.

were the number of fruit ($r_{57} = 0.87$) and fruit weight ($r_{67} = 0.46$, Table 1). The percentage of green fruit and total number of fruit and fruit weight were correlated with marketable yield per plant (Table 2). Percentage of culls was the only yield component not correlated with marketable yield.

All direct effects of the yield components on the yield of marketable tomatoes were significant (Table 2). However, the percentage of culls and marketable yield were not correlated ($r_{48} = 0.02$). This apparent contradiction is explained by breaking down the total correlation into direct and indirect effects. When the strongly negative direct effect of percentage of culls on marketable yield [$P_{48} = (-0.59)$, Table 2] was combined with the positive indirect effect via percentage of green fruit ($r_{34}P_{38} = 0.53$), the result was the weakly positive correlation of percentage of culls with marketable yield ($r_{48} = 0.02$). Simple correlations alone would have lead to the erroneous conclusion that the percentage of culls does not affect marketable yield; our path analysis demonstrates that decreasing the percentage of culls through breeding or cultural practices can greatly increase marketable yield.

The largest compound path coefficients for both total and marketable yields were via total number of fruit (Table 3). Increasing population density of eastern black nightshade decreased total number of fruit more than that of black nightshade. Compound paths via percentage of green fruit were positive for marketable yield with a path coefficient of 0.25 for eastern black nightshade and 0.23 for black nightshade. Summing the path coefficients of

Table 2. Path analysis of the effects of the yield components on marketable yield of tomatoes (kg/plant). Significance levels are presented for the coefficient of determination, direct effects, and simple correlations only.^z

Pathway	Coefficient
Green fruit (%) vs. marketable yield	
Direct effect, P_{38}	-0.82**
Indirect effect via culls (%), $r_{34}P_{48}$	0.38
Indirect effect via total fruit (no.), $r_{35}P_{58}$	0.27
Indirect effect via fruit weight, $r_{36}P_{68}$	-0.08
Total correlation, r_{38}	-0.25*
Culls (%) vs. marketable yield	
Direct effect, P_{48}	-0.59**
Indirect effect via green fruit (%), $r_{34}P_{38}$	0.53
Indirect effect via total fruit (no.), $r_{45}P_{58}$	-0.02
Indirect effect via fruit weight, $r_{46}P_{68}$	0.10
Total correlation, r_{48}	0.02
Total fruit (no.) vs. marketable yield	
Direct effect, P_{58}	0.84**
Indirect effect via green fruit (%), $r_{35}P_{38}$	-0.26
Indirect effect via culls (%), $r_{45}P_{48}$	0.01
Indirect effect via fruit weight, $r_{56}P_{68}$	0.00
Total correlation, r_{58}	0.59**
Fruit weight vs. marketable yield	
Direct effect, P_{68}	0.49**
Indirect effect via green fruit (%), $r_{36}P_{38}$	0.14
Indirect effect via culls (%), $r_{46}P_{48}$	-0.12
Indirect effect via total fruit (no.), $r_{56}P_{58}$	-0.01
Total correlation, r_{68}	0.50**
Coefficient of determination (R^2)	0.92**
Residual, U	0.28

^zThe normal equations for the relationships are in the general form $r_{ij} = P_{ij} + \sum w_k r_{ki} P_{kj}$.

***Significant at $P \leq 0.05$ or 0.01, respectively. All other direct effects or simple correlations were nonsignificant.

the compound paths showed that eastern black nightshade population density explained three times as much of the variability for total yield as black nightshade population density (-0.73 vs. -0.26). Likewise, eastern black nightshade population density accounted for much more of the variability and thus a much greater decline in marketable tomato yield than black nightshade population density (-0.55 vs. -0.02; McGiffen et al., 1992a, 1992b).

The differences in the effect of black or eastern black nightshade density on total or marketable yield can be explained by the competitive ability of each weed species. The greatest effect of nightshade competition on yield comes before the mature-green ripeness stage (McGiffen et al., 1992a). Nightshade shading during anthesis and fruit initiation decreased the total number of tomatoes per plant (McGiffen et al., 1992a; Perez and Masiunas, 1990). Eastern black nightshade is taller than black nightshade and thus competes more effectively with tomato for light, a response leading to a greater decrease in total number of fruit (McGiffen et al., 1992a).

Differences in results of studies on the effect of nightshade population density on tomato yield and percentage of green fruit may be due to indirect effects from correlated yield components. If only the number of tomatoes were reported, nightshade population density effects on other yield components might be obscured. For example, in our study the percentage of green fruit was correlated with percentage of culls and total number of fruit (Fig. 1). Thus, fewer green fruit would be associated with decreased fruit quality [i.e., with a larger percentage of culls; $r_{34} = (-0.65)$] and

Table 3. Compound paths for the effect of black or eastern black nightshade population density on total or marketable tomato yields. Compound paths via correlations between yield components were not determined.^z

Connecting path	Coefficient
Eastern black nightshade vs. total yield via	
Green fruit (%), $P_{13}P_{37}$	0.00
Culls (%), $P_{14}P_{47}$	0.01
Total fruit (no.), $P_{15}P_{57}$	-0.68
Fruit weight, $P_{16}P_{67}$	-0.06
Sum of compound paths	-0.73
Black nightshade vs. total yield via	
Green fruit (%), $P_{23}P_{37}$	0.00
Culls (%), $P_{24}P_{47}$	0.00
Total fruit (no.), $P_{25}P_{57}$	-0.37
Fruit weight, $P_{26}P_{67}$	0.11
Sum of compound paths	-0.26
Eastern black nightshade vs. marketable yield via	
Green fruit (%), $P_{13}P_{38}$	0.25
Culls (%), $P_{14}P_{48}$	-0.08
Total fruit (no.), $P_{15}P_{58}$	-0.66
Fruit weight, $P_{16}P_{68}$	-0.06
Sum of compound paths	-0.55
Black nightshade vs. marketable yield via	
Green fruit (%), $P_{23}P_{38}$	0.23
Culls (%), $P_{24}P_{48}$	-0.01
Total fruit (no.), $P_{25}P_{58}$	-0.35
Fruit weight, $P_{26}P_{68}$	0.11
Sum of compound paths	-0.02

^zNo significance levels are reported for these data because tests of significance have not been developed for compound paths.

increased total number of fruit ($r_{35} = 0.32$).

The compound path for the effect of nightshade population density through percentage of green fruit on marketable fruit yield (Table 3) had a small, positive coefficient for either weed species: black, 0.23; eastern black nightshade, 0.25. This result supports previous findings that nightshade competition for water increases the number of marketable tomatoes by decreasing the percentage of green fruit (McGiffen et al., 1992b). However, the effect of nightshade population density on total number of fruit was larger and in the opposite direction than that on percentage of green fruit (compound path coefficient for black or eastern nightshade population density vs. marketable yield via total number of fruit, -0.66). As a result, there was a net negative effect on marketable yield that obscured the direct positive effect of percentage of green fruit (sum of compound paths for black nightshade vs. marketable yield, -0.02; for eastern black nightshade, -0.55). Thus, while McGiffen et al. (1992b) found that nightshade competition could increase the number of marketable fruit, the overwhelming effect is reduced total tomato yield.

Our path analysis indicated that factors that enhance total fruit set, increase maturity (decrease percentage of green fruit) and decrease the percentage of culls could increase marketable yield. Fruit set could be enhanced by breeding for increased number of flowers, reduced flower abortion, and greater fruit load. Improved early-season management to increase tomato productivity (McAvoy and Janes, 1989) and reduce competition for light (McGiffen, et al., 1992a) also could enhance fruit set. Early-maturing cultivars or properly timed applications of (2-chloroethyl) phosphoric acid (ethephon) could increase the percentage of ripe fruit at harvest. Our path analysis also indicated that breeding for large fruit may

increase the percentage of culls ($r_{46} = 0.21$, Fig. 1). Irrigation during fruit development influences fruit weight (Cannel and Asbell, 1974; Sanders et al., 1989), and could affect the numbers of culls and green fruit. Our results indicated that the percentage of culls and green fruit have a greater impact on marketable yield than total yield per plant. Thus, disease and insect management to reduce the percentage of culls, are important for meeting USDA grading standards and maintaining marketable yield.

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