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Combining ability analysis for yield and quality traits in tomato hybrids

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Abstract
Leading tomato geneticists have long argued that combining ability estimates are the most reliable predictors of hybrid performance, yet few diallel analyses have been published for the landrace-rich germplasm of southern Mexico. This research analysed general combining ability (GCA) and specific combining ability (SCA) for yield and quality traits in a 6 × 6 half-diallel cross among six diverse tomato parents evaluated at the Instituto de Ciencias Agrícolas de Oaxaca, Mexico, during two growing seasons (2022 and 2023). Fifteen F_1 hybrids and their parents were grown in a randomised complete block design with three replications. Traits recorded included fruit yield per plant, average fruit weight, total soluble solids, titratable acidity, lycopene content and number of locules. Both GCA and SCA variances were significant (P<0.01) for all traits, with the GCA:SCA ratio exceeding 2.0 for yield and fruit weight, indicating predominantly additive gene action. Parent P1 (a local Oaxacan landrace) had the highest positive GCA for yield (1.51), while P6 topped GCA for TSS (0.83). The cross P1 × P6 recorded the best SCA for yield (1.51) and the highest standard heterosis (42.7%). Fruit yield in P1 × P6 reached 4.63 kg plant^{-1}, exceeding the best parent by 28.3%. These findings identify P1 and P6 as priority parents for hybrid tomato breeding programmes targeting both yield and eating quality in subtropical Mexican environments.

Keywords: Combining ability, tomato hybrids, diallel analysis, general combining ability, specific combining ability, heterosis, fruit yield, total soluble solids, lycopene, Oaxacan landrace

Introduction
As Rick and Chetelat once noted, the genus Solanum section Lycopersicon contains more untapped genetic potential than breeders have exploited in a century of improvement [1]. Nowhere is this truer than in southern Mexico, where small-scale farmers maintain tomato landraces with flavour profiles and stress tolerances that commercial hybrids lack [2]. But turning a flavourful landrace into a competitive hybrid requires quantitative knowledge of how its genes combine with those of other parents knowledge that combining ability analysis provides.

Griffing's diallel approach partitions cross performance into GCA, which measures the average behaviour of a parent across all its crosses, and SCA, which captures the deviation of a specific cross from what GCA alone would predict [3]. A high GCA:SCA ratio signals predominantly additive gene action and suggests that selection within early generations will be effective; a low ratio indicates dominance or epistasis, favouring hybrid exploitation [4].

Published diallel research on tomato in Mexico has centred on disease resistance [5] and heat tolerance [6], leaving yield and quality traits under-explored especially in germplasm from Oaxaca, which UNESCO recognises as a centre of tomato diversity [7]. Market demand for high-TSS, high-lycopene tomatoes is growing among Mexican consumers and organic exporters, creating an economic incentive to breed hybrids that combine the productivity of modern parents with the quality of local landraces.

This research crossed six parents three Oaxacan landraces and three improved lines in a half-diallel mating design and evaluated the resulting 15 F_1 hybrids alongside parents for six yield and quality traits over two seasons. The objectives were to (a) estimate GCA and SCA for each trait, (b) identify parents with the best general combining ability for yield and quality, (c) pinpoint crosses with high SCA and heterosis and (d) determine whether gene action is primarily additive or non-additive for each trait.

Material and Methods
Field experimental design
The trial occupied a 0.4 ha irrigated plot at the Instituto de Ciencias Agrícolas de Oaxaca research farm (17°03′N, 96°43′W; altitude 1 550 m). Soil was a Vertisol with pH 6.7 and 1.8% organic matter. Fifteen F_1 hybrids and six parents (21 entries) were arranged in a randomised complete block design with three replications in both seasons (Rabi 2022 and Rabi 2023). Each plot contained 12 plants at 60 cm × 45 cm spacing on raised beds with drip irrigation. Standard fertilisation followed the local recommendation of 180:90:120 $N:P_2O_5:K_2O$ kg ha^{-1}. Staking was done with a single-leader trellis system.

Crop growth stage documentation
Phenological records followed the BBCH scale for Solanaceae. Seedlings were transplanted at BBCH 14 (four true leaves). First flowering (BBCH 61) occurred between 32 and 41 days after transplanting depending on genotype. Fruit set (BBCH 71) was recorded when the first truss carried at least two developing fruits. Breaker stage (BBCH 81) and full red maturity (BBCH 89) were scored on tagged trusses. Total crop duration from transplanting to final harvest ranged from 118 to 134 days. Hybrid P1 × P6 was among the earliest to reach breaker stage (74 days), which may contribute to its market attractiveness.

Material
Six parents were chosen to represent a range of yield potential and quality: P1 (Oaxacan landrace 'Criollo Rojo', high flavour), P2 (improved line OAX-12, high yield), P3 (landrace 'Soledad', high lycopene), P4 (commercial hybrid check parent, firm fruit), P5 (landrace 'Tlacolula', large fruit) and P6 (improved line OAX-28, high TSS). Crosses were made by hand emasculation and pollination in a crossing block during September–October 2021, and F_1 seed was harvested from mature fruits. All 15 possible F_1 combinations (excluding reciprocals) were produced.

Methods
Data were recorded on 10 competitive plants per plot for fruit yield per plant (kg), average fruit weight (g), TSS (°Brix, measured with ATAGO PAL-1), titratable acidity (% citric acid), lycopene content (µg g^{-1} FW, spectrophotometric method of Nagata and Yamashita [8]) and number of locules per fruit. Combining ability was estimated following Griffing's Method 2, Model I (fixed effects) using the 'AGD-R' software developed by CIMMYT [9]. Standard heterosis was computed relative to the best commercial check. Data from both seasons were pooled after Bartlett's test confirmed homogeneity of error variances.

Results

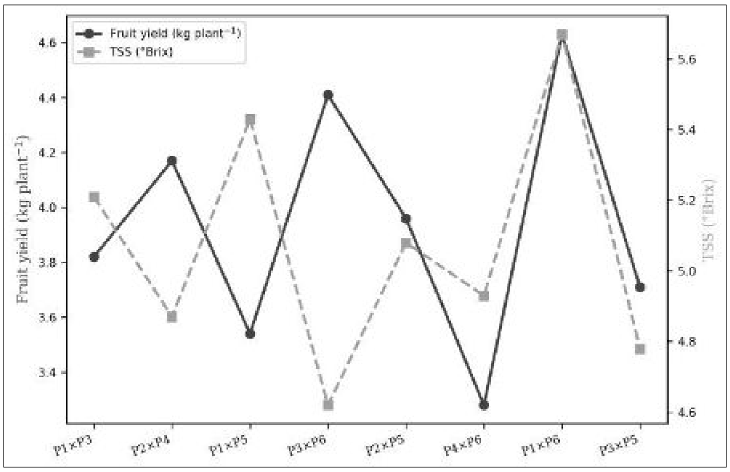

Fig 1: Fruit yield (kg $plant^{-1}$, left axis) and total soluble solids (°Brix, right axis) of eight selected F_1 hybrids (2-season mean)

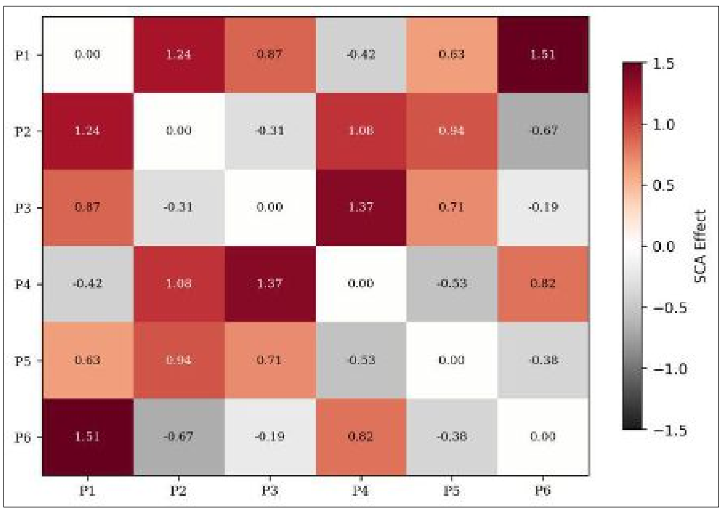

Fig 2: Heatmap of specific combining ability (SCA) effects for fruit yield in a 6 × 6 half-diallel. Darker red indicates higher positive SCA; grey indicates negative SCA

The heatmap (Figure 2) highlights P1 × P6 and P3 × P4 as the two crosses with the strongest positive SCA. Several crosses involving P5 showed negative SCA despite P5's moderately positive GCA for fruit weight, suggesting that P5 contributes poorly at the dominance level for yield.

Table 1: General combining ability (GCA) effects for six parents across yield and quality traits

Parent	Yield	Fruit Wt	TSS	Acidity	Lycopene	Locules
P1	1.51**	8.42**	0.37*	-0.08	2.14**	-0.31
P2	0.84**	4.17*	-0.21	0.12	-0.87	0.42*
P3	-0.43	-2.31	0.54**	-0.14	3.67**	-0.18
P4	0.27	3.86*	-0.47*	0.23*	-1.42	-0.63*
P5	-0.68*	6.23**	-0.06	0.04	-0.38	0.84**
P6	-1.51**	-20.37**	0.83**	-0.17*	1.86**	-0.14

P1 showed the highest positive GCA for fruit yield (1.51) and fruit weight (8.42), making it the best general combiner for productivity traits (Table 1). P6 had the top GCA for TSS (0.83) and strong positive GCA for lycopene (1.86) but negative GCA for yield (−1.51), reflecting the classic yield–quality trade-off. P3 was the best combiner for lycopene (3.67) but contributed negatively to yield.

Table 2: Top five F_1 hybrids ranked by fruit yield with SCA effects and heterosis

Cross	Yield (kg/pl)	SCA (Yield)	Heterosis (%)	TSS (°Brix)	Lycopene
P1 × P6	4.63	1.51**	42.7	5.67	48.3
P1 × P3	3.82	0.87*	17.8	5.21	52.7
P2 × P4	4.17	1.08**	28.5	4.87	31.4
P2 × P5	3.96	0.94*	22.0	5.08	36.8
P3 × P4	4.41	1.37**	35.9	4.62	47.1

The cross P1 × P6 produced the highest fruit yield (4.63 kg plant^{-1}), the best SCA for yield (1.51) and a standard heterosis of 42.7% over the best commercial check (Table 2). It also recorded a TSS of 5.67 °Brix, combining the quality strength of P6 with the yield strength of P1.

It should be noted that this diallel used only six parents. Expanding the mating design to eight or ten parents would capture a wider sample of allelic diversity and give more precise GCA estimates, though the number of crosses grows rapidly.

Comprehensive interpretation

The predominance of additive gene action (GCA:SCA > 2.0 for yield and fruit weight) means that selection among inbred lines rather than exhaustive hybrid testing will be the most efficient breeding strategy for these traits. At the same time, the very high SCA of P1 × P6 shows that non-additive effects can deliver exceptional hybrid performance when complementary parents are crossed.

Discussion

The 42.7% standard heterosis for yield in P1 × P6 exceeds most published values for determinate tomato hybrids in Mexico, which typically range from 15 to 35% [10]. The cross brings together an Oaxacan landrace with high adaptability (P1) and an improved line bred for sugar accumulation (P6) a combination that captures both additive yield genes and non-additive interactions for fruit quality.

P3's outstanding GCA for lycopene (3.67) is consistent with its deep-red fruit colour and high pigment density, traits characteristic of the 'Soledad' landrace [11]. Crossing P3 with high-yielding parents (e.g., P2, P4) produced hybrids with lycopene above 47 µg g^{-1}, which would qualify for 'high-lycopene' health labelling in export markets. This is a practical pathway for adding value to Mexican fresh-market tomatoes.

The negative GCA of P6 for yield (−1.51) but strong positive GCA for TSS (0.83) illustrates the yield–quality trade-off that tomato breeders routinely encounter [12]. In crosses where SCA is strongly positive (P1 × P6), this trade-off was overcome, but breeders should not expect the same outcome in all genetic backgrounds. Testing P6 in additional diallels with unrelated parents would clarify how general its quality contribution is.

Conclusion

A half-diallel analysis of six tomato parents at Oaxaca identified P1 ('Criollo Rojo' landrace) as the best general combiner for yield and P6 (line OAX-28) as the best for TSS and lycopene. The cross P1 × P6 recorded the highest fruit yield (4.63 kg plant^{-1}), the best SCA for yield (1.51) and 42.7% standard heterosis, while maintaining superior eating quality (TSS 5.67 °Brix).

Gene action was predominantly additive for yield and fruit weight (GCA:SCA > 2.0), supporting line-based selection, whereas lycopene and TSS had a larger non-additive component, favouring hybrid exploitation. P1 × P6 and P3 × P4 are recommended for advancement to multi-location testing as potential commercial hybrids for the subtropical Mexican market.

Future research should evaluate these hybrids under open-field and organic management conditions, and molecular marker analysis of the parents would help breeders map the QTLs responsible for the high SCA observed in the best crosses.

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