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RESEARCH

An Introgression from Wild Tomato (*Solanum habrochaites*) Affects Tomato Photosynthesis and Water Relations

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ABSTRACT

A quantitative trait locus (QTL) *stm9* (shoot-turgor maintenance; located on chromosome 9) from chilling-tolerant *Solanum habrochaites* S. Knapp & D.M. Spooner maintains plant water status via stomatal closure in response to root chilling, which induces a rapid onset form of root water stress. Here we examined the effect of an introgressed *S. habrochaites* chromosome 9 region, which contains QTL *stm9*, on water relations, photosynthesis, and yield in the field. Three near-isogenic lines (NILs) of cultivated tomato (*Solanum lycopersicum* L.) with and without *S. habrochaites* chromosome 9 introgressions, and their parent cultivar T5, were evaluated in 2 yr of field experiments in Davis, CA. The NILs with a *S. habrochaites* introgression exhibited predawn and midday leaf conductances that were 23 and 10% smaller, respectively, than those of the NIL without the *S. habrochaites* introgression and the parent cultivar. This resulted in the NILs with the *S. habrochaites* region having 23% higher predawn leaf water potential, 13% higher midday leaf water potential, and 13% lower net photosynthesis than the NIL without the *S. habrochaites* introgression and the parent cultivar. Yield in the NILs containing small (NIL175) and large (NIL1322) introgressions of *S. habrochaites* decreased an average of 42 and 71%, respectively, compared with the NIL without the introgression and the parent cultivar. The effect of the introgression from *S. habrochaites* under nonchilling conditions may prove useful for understanding tradeoffs between productivity and transpiration.

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Abbreviations: ETc, crop evapotranspiration; NIL, near-isogenic line; NW, nonwilting; QTL, quantitative trait locus; UC, University of California; W, wilting.

Chilling temperatures below 12°C but above freezing severely restrict water movement from plant roots to shoots (Hales, 1727). Cultivated tomato (*Solanum lycopersicum* L.) originates from the wet tropics of South America (Rick, 1976; Nakazato et al., 2010). Like many plants of tropical and subtropical origin, cultivated tomato suffers slower growth and significant injury at chilling temperatures (Geisenberg and Stewart, 1986). In contrast, *S. habrochaites*, an interfertile wild tomato that grows at high elevations in the Peruvian Andes, thrives despite monthly minimum temperatures of less than 5°C year round (Hijmans et al., 2005). This differential chilling sensitivity derives in part from stomatal responses to root chilling: cultivated tomato fails to close its stomata rapidly in response to root chilling, its transpiration rate exceeds water transport to the shoot, and it suffers rapid shoot wilting, whereas *S. habrochaites* rapidly closes its stomata and avoids injury (Hales, 1727; Wilson, 1976; Markhart et al., 1979; Bagnall et al., 1983; Fennell and Markhart, 1998; Truco et al., 2000; Aroca et al., 2001; Bloom et al., 2004; Goodstal et al., 2005).

A major quantitative trait locus (QTL) for shoot-turgor maintenance under root chilling obtained from *S. habrochaites* accession LA1778 was detected and fine-mapped on chromosome 9 and denoted as *stm9* (Truco et al., 2000; Goodstal et al., 2005). *S. habrochaites* acc. LA1778 was collected at 2950 m above sea level

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in a Peruvian Andes habitat with monthly minimum temperatures of less than 2°C and a mean annual precipitation of 641 mm yr^{-1} (Hijmans et al., 2005). This extreme environment is typical of *S. habrochaites* accessions, although some accessions can be found at lower elevations (Easlon et al., 2013). Near-isogenic lines (NILs) that contain a chromosome 9 region from *S. habrochaites* acc. LA1778, which includes QTL *stm9* in an otherwise *S. lycopersicum* cv. T5 genomic background, maintain shoot turgor during root chilling to a similar extent as the parental high-elevation *S. habrochaites* accession (Goodstal et al., 2005). The temperature sensitivity of root hydraulic conductance was similar in both species; therefore, shoot-turgor maintenance in *S. habrochaites* derived from rapid stomatal closure rather than from differences in water supply from the roots (Bloom et al., 2004). This stomatal response to root chilling is similar to the response of some wild tomato species to drought in that these species are typically deep rooted and regulate stomata to maintain high plant-water status during drought (Kebede et al., 1994; Torrecillas et al., 1995; Easlon and Richards, 2009).

A preliminary field experiment suggested that the NILs described above maintained a higher leaf water potential under nonchilling conditions. Rapid stomatal closure in response to root chilling, which we have observed in wild tomato species from high elevations (Bloom et al., 2004), may also result in lower stomatal conductance under nonchilling conditions. Low stomatal conductance may decrease water stress during drought but may also limit photosynthesis and thereby decrease productivity (Sinclair and Purcell, 2005). Here, we compare NILs of *S. lycopersicum* without and with *S. habrochaites* LA1778 chromosome 9 introgressions that include QTL *stm9* to assess the impact of this chromosome region on plant water relations, photosynthesis, and yield in plants grown during two field seasons.

MATERIALS AND METHODS

Plant Materials

We employed cultivated *S. lycopersicum* cultivar T5 and three NILs derived from the parent line T5 via marker-assisted backcrossing containing chromosome 9 introgressions that include the QTL *stm9* region from *S. habrochaites* acc. LA1778 in an otherwise *S. lycopersicum* cv. T5 genomic background (verified by molecular markers). NIL 03GH1322 (denoted as NIL1322) and NIL 09GH0175 (NIL175) do not wilt (i.e., no loss of shoot turgor) under root chilling (Goodstal et al., 2005; data not shown) and served as the nonwilting genotypes. NIL1322 has *S. habrochaites* alleles at all chromosome 9 markers in the interval TG254 to T1617 (Fig. 1; Goodstal et al., 2005), a larger region than in NIL175, which contains *S. habrochaites* alleles at all markers in the interval TG18 to T532 (Fig. 1). NIL 09GH0163 (NIL163) was obtained as a segregant from the same parent as NIL175 but instead carries *S. lycopersicum* cv. T5 alleles at all chromosome 9 markers (Fig. 1). Therefore, NIL163 and NIL175 are

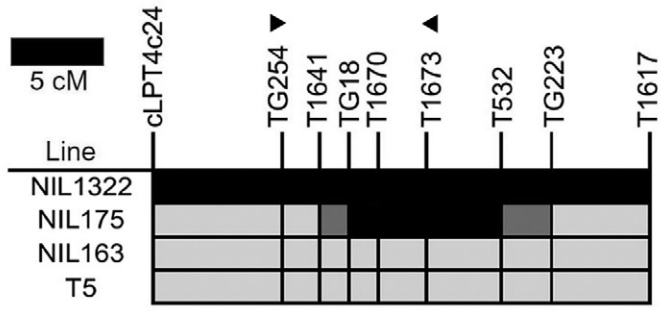

Figure 1. Graphical representation of chromosome 9 marker genotypes for the four tomato lines used in this study. Arrows indicate the approximate fine-mapped location of QTL *stm 9* from Goodstal et al. (2005). Light gray bars indicate regions homozygous for *S. lycopersicum* alleles, black bars indicate regions homozygous for *S. habrochaites* alleles, and dark grey bars indicate regions of recombination breakpoints.

closely related, or "paired," NILs. NIL163 and the T5 parent line wilt under root chilling (Bloom et al., 2004) and served as the wilting controls (W). Seeds of cultivar T5 (TGRC accession LA2399) are available by request from the Tomato Genetics Resource Center (http://tgrc.ucdavis.edu). The NILs used in this study are experimental breeding lines; seeds are available by request from D. St.Clair.

Field Experimental Design and Procedures

Seeds of all lines were germinated in flats containing a peat-based medium in a greenhouse at the University of California (UC) Davis. Greenhouse temperatures were 25–35°C during the day and 18–25°C during the night. After 21 d, the seedling flats were transferred to a lath house to harden off for 1 to 3 wk before field transplanting at the UC Davis Plant Sciences Department field research facility (located at 38° 32′ N, 121° 46′ W; USDA soil classification: fine-silty, mixed, nonacid, thermic Typic Xerorthent). Planting beds with a width of 1.5 m were prepared with one 8-mm drip line per row buried at a depth of 20 cm with 0.61 L h^{-1} emitters spaced every 0.3 m. Planting beds were prepared in the spring as soon as the top layers of soil dried enough to prevent compaction during cultivation. Seedlings were transplanted by hand to the field on 29 April 2011 and 17 May 2012. Seedlings were transplanted in a single row down the center of each 1.5-m bed, and plants were spaced 0.6 m apart (1.11 plant m^{-2}) in a split-plot experimental design. The main plot treatments were irrigations of 100, 75, and 50% of crop evapotranspiration (ETc) in 2011 and 100 and 50% of ETc in 2012. Main plots (irrigation treatments) were replicated three times in each of the 2 yr. Planted within each main plot (irrigation treatment) were four and six replications of subplots in 2011 and 2012, respectively. The subplots contained four plants for each of the four genotypes: nonwilting (NW) NIL1322 and NIL175 and wilting (W) NIL163 and T5. Each main plot irrigation treatment was bordered by two rows of tomato plants on which no measurements were made. After allowing plants to establish for 4 wk, irrigation treatments were started on 4 June 2011 and 17 June 2012. CIMIS reference evapotranspiration calculations from a neighboring weather station (www.cimis.water.ca.gov) and tomato crop coefficient

Table 1. Mean leaf water potentials (Ψ), midday photosynthesis (*A*), midday leaf conductance (*g*), and nighttime leaf conductance (g_{night}) for lines and wilting (W) and nonwilting (NW) groups in 2011 and 2012 field seasons in Davis, CA.

Line	predawn Ψ	midday Ψ	*A*	*g*	g_{night}
	MPa		μmol m^{-2} s^{-1}	mol m^{-2} s^{-1}	
2011					
T5	−0.15 ± 0.01 a†	−0.82 ± 0.05	19.4 ± 0.5 ab	0.51 ± 0.04	0.09 ± 0.01
NIL163	−0.16 ± 0.01 a	−0.81 ± 0.04	21.3 ± 1.0 a	0.54 ± 0.03	0.09 ± 0.01
NIL175	−0.12 ± 0.01 b	−0.69 ± 0.02	16.7 ± 1.1 ab	0.47 ± 0.04	0.07 ± 0.01
NIL1322	−0.11 ± 0.01 b	−0.71 ± 0.03	17.1 ± 1.3 b	0.47 ± 0.04	0.07 ± 0.01
W group	−0.16 ± 0.01 x	−0.81 ± 0.03 x	20.5 ± 0.6 x	0.52 ± 0.02	0.09 ± 0.01 x
NW group	−0.12 ± 0.01 y	−0.70 ± 0.02 y	16.9 ± 0.9 y	0.47 ± 0.03	0.07 ± 0.01 y
2012					
T5	−0.20 ± 0.01 a	−1.08 ± 0.03 a	26.4 ± 0.8	0.66 ± 0.03	0.09 ± 0.01 a
NIL163	−0.19 ± 0.01 a	−1.09 ± 0.03 a	27.3 ± 0.8	0.67 ± 0.03	0.07 ± 0.01 ab
NIL175	−0.16 ± 0.01 b	−0.95 ± 0.03 b	24.5 ± 1.1	0.59 ± 0.03	0.06 ± 0.01 b
NIL1322	−0.15 ± 0.01 b	−0.96 ± 0.04 b	24.3 ± 1.1	0.59 ± 0.02	0.06 ± 0.01 b
W group	−0.20 ± 0.005 x	−1.09 ± 0.02 x	26.9 ± 0.5 x	0.66 ± 0.02 x	0.08 ± 0.01 x
NW group	−0.16 ± 0.005 y	−0.95 ± 0.02 y	24.4 ± 0.7 y	0.59 ± 0.02 y	0.06 ± 0.01 y

†Letters denote statistically significant differences according to Tukey's test ($P \leq 0.05$) between lines or W and NW groups.

recommendations were used to determine weekly irrigation duration. Plants were fertigated weekly with $Ca(NO_3)_2$ at 3.6 kg ha^{-1} of N. Weed and pest control were performed according to standard tomato management practices.

Field Trait Data Collection and Methods

Leaf water potentials (Ψ) at predawn (0400 to 0500 h) and midday (1100 to 1300 h) were assessed weekly from 13 July to 8 August in 2011 and 2012 with a PMS 1000 pressure chamber (PMS Instrument, Albany, OR). These samplings occurred after canopy closure to minimize the effects of leaf harvest on growth. On each date, two young, fully expanded, sun-exposed leaves were assessed for each subplot.

Leaf net photosynthesis (*A*) and conductance (*g*) were measured on young, fully expanded leaves in a LI-6400 standard leaf cuvette (LiCor, Lincoln, NE) set at ambient temperature and CO_2 concentration. On 2 August 2011 and 27 July 2012, nighttime leaf conductance (g_{night}) was measured in the darkness from 0200 to 0400 h on one plant per subplot. On 2 August 2011 and 3 August 2012, *A* and *g* were measured from 1000 to 1400 h at 1500 μmol m^{-2} s^{-1} photosynthetic photon flux density on one plant per subplot.

We collected 12 to 15 young, fully expanded, sun-exposed leaves per genotype and irrigation treatment on 8 August in 2011 and 2012. Leaf samples were dried for at least 72 h at 60°C, ground, and subsampled for further analysis. One subsample was analyzed for C and N content and stable carbon isotope composition ($\delta^{13}C$; $^{13}C/^{12}C$ relative to Pee Dee Belemnite standard) at the UC Davis Stable Isotope Facility (http://stableisotopefacility.ucdavis.edu/). The other subsample was analyzed for total macro- and micronutrients at the UC Davis Analytical Laboratory (http://anlab.ucdavis.edu/).

All fruit showing color was harvested by hand weekly from 10 August to 6 September in 2011 and 24 August to 14 September in 2012. Each year, fruit harvest was terminated once productivity sharply declined and very few fruits remained. The number of fruits and fruit fresh weight of marketable fruit (intact and larger than 5 cm in diameter) were recorded. The total yield for each year was obtained as the sum of all weekly harvests.

Data Analyses

The experimental design in both 2011 and 2012 was a split-plot design with four and six replicates respectively, with irrigation treatment as main plots and genotypes as subplots. Analysis of variance (ANOVA) was performed separately for each year via PROC MIXED (SAS version 9.3, SAS Institute, Cary, NC) with irrigation treatment, genotype and genotype × irrigation treatment as fixed effects, and block and block × irrigation treatment as random effects. Mean separations by genotype or by groups, NW (NIL175 and NIL1322) versus W (NIL163 and T5), were determined using Tukey's tests ($P < 0.05$). Pearson correlation coefficients were used to examine the relationship between leaf $\delta^{13}C$ and yield and between leaf $\delta^{13}C$ and leaf carbon percentage (%C) on genotype means for 2011 and for 2012 using SigmaPlot 11 (Systat, Richmond, CA).

RESULTS

There were no significant differences detected among the water treatments (100, 75, and 50% ETc in 2011 or between 100 and 50% ETc in 2012) for the traits measured; therefore, subsequent analyses focused on testing for differences among genotypes. In general, the four genotypes responded as two groups: those with the *S. habrochaites* chromosome 9 introgression (NIL175, NIL 1322) and those without (NIL163, T5). More specifically, there were few differences between the performance of NIL175 and NIL1322, which do not wilt during root chilling, and no differences between the performance of NIL163 and T5, which wilt (Table 1).

The NW genotypes NIL175 and NIL1322 had a higher plant water status in the field compared with the W genotypes NIL163 and T5 in both years. Throughout the season, predawn and midday leaf Ψ were less negative in the NW genotypes than in the W genotypes (2011: predawn, $P < 0.0001$; midday, $P = 0.0021$; 2012: predawn, $P < 0.0001$; midday, $P = < 0.0001$) (Table 1). Predawn and midday leaf water potentials were more negative in 2012

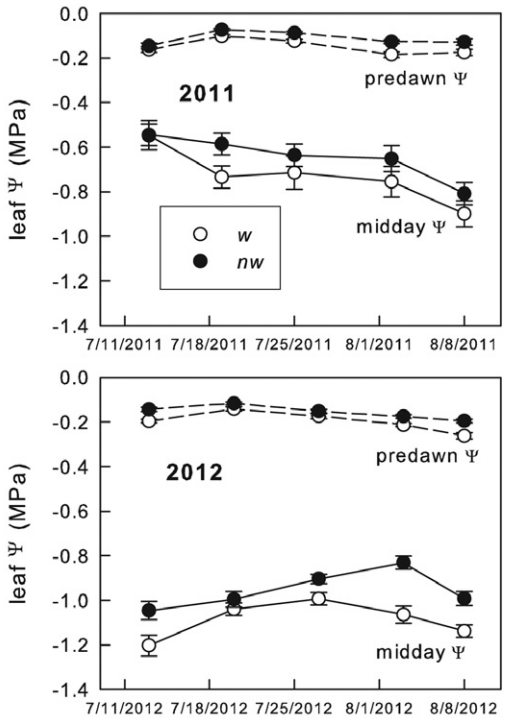

Figure 2. Mean (± standard error) predawn and midday leaf water potential (Ψ) of wilting (open symbols) and nonwilting (filled symbols) genotypes during 2011 and 2012 field seasons in Davis, CA.

(irrigated at between 100 and 50% ETc) than 2011 (irrigated at 100, 75, and 50% ETc) (Fig. 2).

Leaf conductance at night (g_{night}) in all genotypes was greater than cuticular conductance (0.01 mol m^{-2} s^{-1} for *S. lycopersicum*; Caird et al., 2007), indicating incomplete stomatal closure at night in all genotypes. The g_{night} was 21% (P = 0.0262) and 25% (P = 0.0025) lower in NW genotypes than in W genotypes in 2011 and 2012 (Table 1). Midday leaf conductance, g, was lower in NW genotypes than in W genotypes in 2012 but were not lower in 2011 (2011: P = 0.1647; 2012: P = 0.0019). Midday net A was lower in NW plants than in W genotypes in both years (2011: P = 0.0034; 2012: P = 0.0047) (Table 1).

Leaf $\delta^{13}C$ was less negative in NW genotypes than in W genotypes in both years (2011: $P < 0.0001$; 2012: $P < 0.0001$) (Fig. 3). Leaf $\delta^{13}C$ was less negative in NIL1322, which contained a larger introgression, than in NIL175 in both years (2011: P = 0.0267; 2012: $P < 0.001$) (Fig. 1, 3). Yield decreased with leaf $\delta^{13}C$ in 2011 and 2012 (Fig. 3a, c). Total fruit yield in NW NIL175 and NIL1322 was reduced 34 and 67% in 2011, and 50 and 74% in 2012 in comparison with the W genotypes NIL163 and T5 ($P < 0.0001$; $P < 0.0001$) (Fig. 3a, c). Weekly yield in the NW genotypes was lower than in the W genotypes across all harvest dates in 2011 and 2012 ($P < 0.05$ for all weekly harvests; Fig. 4). Fruit size was unaffected by the presence of the *S. habrochaites* introgression (Fig. 4).

Leaf %C increased with leaf $\delta^{13}C$ in 2011, although leaf %C in only NIL1322 with the larger introgression from *S. habrochaites* differed from that in the W genotypes in both years ($P < 0.0001$; Fig. 3b, d). Because leaves of highly transpiring plants can accumulate greater concentrations of xylem solutes than leaves of plants with lower transpiration rates, we subtracted the xylem-transported macronutrients Ca, Mg, and S from the total leaf dry weight and recalculated leaf %C to determine if the correlation between leaf %C and leaf $\delta^{13}C$ was due to dilution of leaf %C in highly transpiring plants. Such an adjustment had little effect on the slope of the correlation, indicating that dilution minimally contributed to the correlation (Fig. 3b, d).

DISCUSSION

The chromosome 9 *S. habrochaites* introgression influenced Ψ, g, leaf $\delta^{13}C$, A, and yield in plants grown under non-chilling field conditions. During the night, low stomatal conductance and limited evaporative demand usually result in equilibration between soil and leaf Ψ (Boyer and Kramer, 1995). The lack of significant differences in leaf Ψ between irrigation treatments suggests that the tomato plants in all irrigation treatments had access to soil moisture either from wetter soil at depth, from neighboring NW NIL subplots, and/or from neighboring fully irrigated plots across two border rows due to the extensive root systems of tomatoes (Jackson and Bloom, 1990). Early transplanting and late rains in June 2011 may have also allowed deeper rooting to occur before imposing the water-stress treatments. Also the low planting density may have resulted in overestimating ETc before full canopy coverage. The lower water use in NW NILs may have contributed to an overestimate of ETc after full canopy coverage, resulting in a negligible water deficit for all irrigation treatments. The presence of the *S. habrochaites* introgression in NILs resulted in less negative predawn leaf Ψ (Fig. 2), most probably as a result of lower g_{night} in NW plants (Table 1). Although predawn leaf Ψ should reflect soil Ψ, both cultivated and wild tomatoes can have significant stomatal opening at night, which can produce a predawn disequilibrium between soil and leaf Ψ and result in lower predawn leaf Ψ in W plants (Donovan et al., 2001; Caird et al., 2007; Easlon and Richards, 2009).

At midday, when leaf Ψ approaches its lowest value, the NW NILs also maintained a higher plant water status than W genotypes (Fig. 2). This effect on leaf Ψ seems reasonable because the presence of the *S. habrochaites* chromosome 9 region containing QTL *stm9* in NW NILs increased plant water status through stomatal closure during chilling-induced water stress (Bloom et al., 2004; Goodstal et al., 2005). Higher midday leaf Ψ most probably resulted from lower g in NW genotypes, although midday g was not lower in 2011 (Table 1). Additional measurements of g might have clarified differences in stomatal behavior between NILs, but g can be highly variable because g rapidly responds to changing environmental conditions.

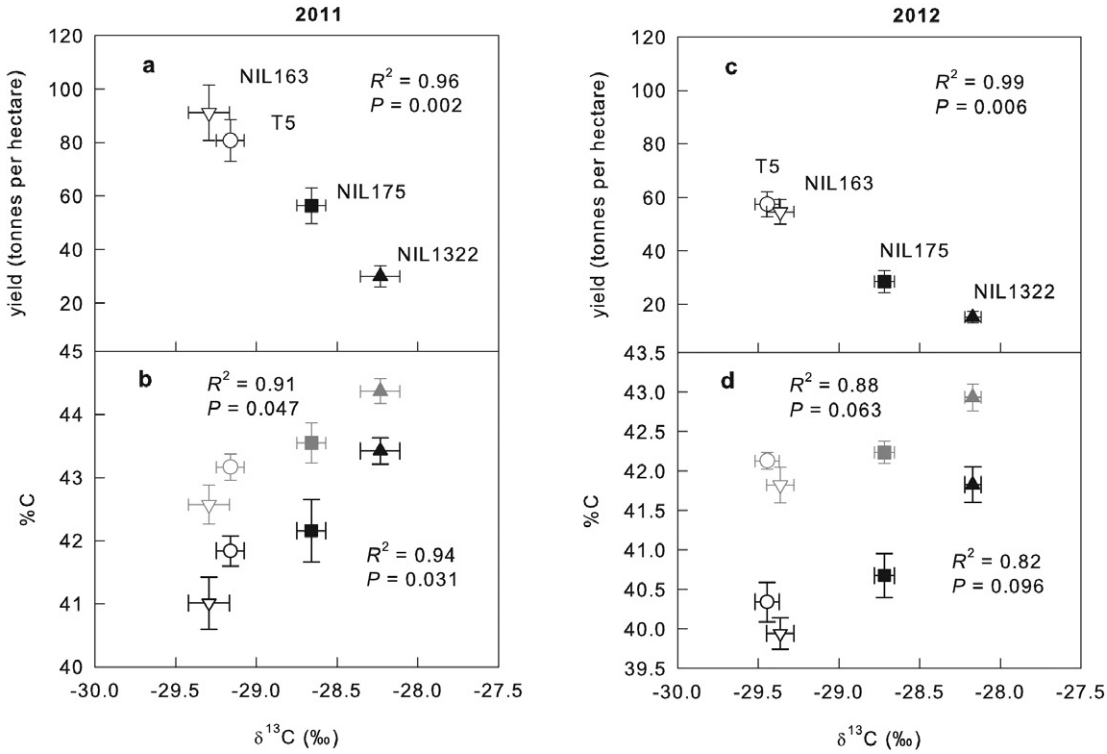

Figure 3. Correlations between leaf carbon isotopic composition ($\delta^{13}C$) and (a, c) yield and (b, d) leaf carbon percentage (%C) in 2011 and 2012 field seasons in Davis, CA. Gray symbols represent %C adjusted for dilution by Ca, Mg, S. Symbols are genotype means (± standard error).

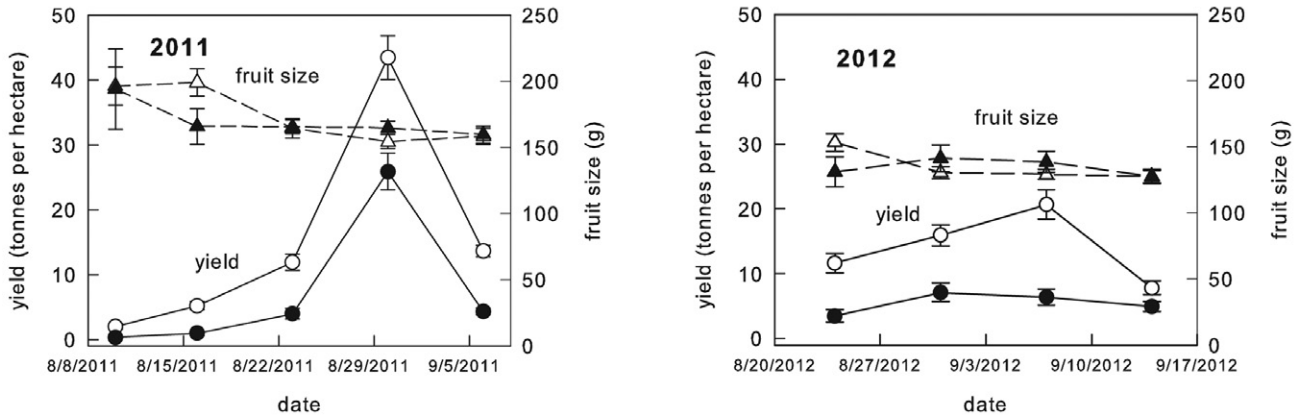

Figure 4. Mean (± standard error) yield (circles) and fruit size (triangles) of wilting (open symbols) and nonwilting (filled symbols) genotypes at each field harvest date for 2011 and 2012 in Davis, CA.

Leaf $\delta^{13}C$ integrates stomatal conductance over the entire growth period of the leaf and is more strongly correlated than leaf gas-exchange measurements with transpiration efficiency throughout the season (Martin and Thorstenson, 1988; Farquhar et al., 1989). Less negative $\delta^{13}C$ in the NW NILs compared with the W genotypes indicates the introgression from *S. habrochaites* reduces season-long stomatal conductance and may increase transpiration efficiency in NW NILs (Fig. 3). Low stomatal conductance and high transpiration efficiency at the leaf level, which occur during nonstress conditions, may adversely limit photosynthesis and crop productivity.

The timing of fruit ripening and average fruit size during the harvest interval were similar in all four genotypes regardless of the absence or presence of the *S. habrochaites* introgression (Fig. 4). Lower yield in the NW NILs may have resulted from stomatal limitations on photosynthesis (Table 1, Fig. 3a, c) and linkage drag effects caused by the presence of other *S. habrochaites* genes linked to QTL *stm9*. In 2011, leaf $\delta^{13}C$ was correlated with leaf %C even after %C was adjusted for dilution by the accumulation of Ca, Mg, and S, which may occur in rapidly transpiring plants (Fig. 3b, d). Lower fruit demand for photosynthate resulting from the *S. habrochaites* introgression could account for higher leaf %C despite lower rates of

photosynthesis (Table 1). Lower fruit demand may also result from the effects of other *S. habrochaites* genes on chromosome 9 in addition to those causal for QTL *stm9*.

Although the presence of the *S. habrochaites* allele at QTL *stm9* is associated with stomatal response to chilling temperatures, the *S. habrochaites* introgression containing QTL *stm9* also affects stomatal conductance under nonchilling conditions in the field. The negative correlation between $\delta^{13}C$ and yield suggests that increases in transpiration efficiency via stomatal conductance alone may not ultimately be beneficial for tomato productivity. Although water deficits reduce yield and fruit size in cultivated tomato (Martin and Thorstenson, 1988; Mitchell et al., 1991), the decrease in yield that may be associated with higher transpiration efficiency may outweigh the benefits of higher plant water status. Differences in $\delta^{13}C$ between the NW NILs suggest that other gene(s) present in the introgressed region in NIL1322 also may contribute to low stomatal conductance and negatively affect productivity. Further analysis of the introgressed *S. habrochaites* region should prove useful for understanding tradeoffs between productivity and transpiration in tomato.

Acknowledgments

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References

Aroca, R., F. Tognoni, J.J. Irigoyen, M. Sanchez-Diaz, and A. Pardossi. 2001. Different root low temperature response of two maize genotypes differing in chilling sensitivity. Plant Physiol. Biochem. 39:1067–1073. doi:10.1016/S0981-9428(01)01335-3

Bagnall, D., J. Wolfe, and R.W. King. 1983. Chill-induced wilting and hydraulic recovery in mung bean plants. Plant Cell Environ. 6:457–464. doi:10.1111/1365-3040.ep11588106

Bloom, A.J., M.A. Zwieniecki, J.B. Passioura, L.B. Randall, N.M. Holbrook, and D.A. St. Clair. 2004. Water relations under root chilling in a sensitive and tolerant tomato species. Plant Cell Environ. 27:971–979. doi:10.1111/j.1365-3040.2004.01200.x

Boyer, J.S., and P.J. Kramer. 1995. Measuring the water status of plants and soils. Academic Press, San Diego, Calif.

Caird, M.A., J.H. Richards, and T.C. Hsiao. 2007. Significant transpirational water loss occurs throughout the night in field-grown tomato. Funct. Plant Biol. 34:172–177. doi:10.1071/FP06264

Donovan, L.A., M.J. Linton, and J.H. Richards. 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well-watered conditions. Oecologia 129:328–335. doi:10.1007/s004420050850

Easlon, H.M., and J.H. Richards. 2009. Drought response in self-compatible species of tomato (Solanaceae). Am. J. Bot. 96:605–611. doi:10.3732/ajb.0800189

Easlon, H.M., J.S.R. Asensio, D.A. St. Clair, and A.J. Bloom. 2013. Chilling-induced water stress: Variation in shoot turgor maintenance among wild tomato species from diverse habitats. Am. J. Bot. doi:10.3732/ajb.1200508

Farquhar, G., J.R. Ehleringer, and K.T. Hubrick. 1989. Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. 40:503–537. doi:10.1146/annurev.arplant.40.1.503

Fennell, A., and A.H. Markhart. 1998. Rapid acclimation of root hydraulic conductivity to low temperature. J. Exp. Bot. 49:879–884. doi:10.1093/jexbot/49.322.879

Geisenberg, C., and K. Stewart. 1986. Field crop management. In: J.G. Atherton and J. Rudich, editors, The tomato crop: A scientific basis for improvement. Chapman and Hall, London. p. 511–557.

Goodstal, F.J., G.R. Kohler, L.B. Randall, A.J. Bloom, and D.A. St. Clair. 2005. A major QTL introgressed from wild *Lycopersicon hirsutum* confers chilling tolerance to cultivated tomato (*Lycopersicon esculentum*). Theor. Appl. Genet. 111:898–905. doi:10.1007/s00122-005-0015-2

Hales, S. 1727. Vegetable Staticks or, An account of some statical experiments on the sap in vegetables: Being an essay towards a natural history of vegetation. Also, a specimen of an attempt to analyse the air, by a great variety of chymio-statical experiments; which were read at several meetings before the Royal Society. W. and J. Innys, T. Woodward, London.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978. doi:10.1002/joc.1276

Jackson, L.E., and A.J. Bloom. 1990. Root distribution in relation to soil nitrogen availability in field-grown tomatoes. Plant Soil 128:115–126. doi:10.1007/BF00011100

Kebede, H., B. Martin, J. Nienhuis, and G. King. 1994. Leaf Anatomy of 2 *Lycopersicon* species with contrasting gas-exchange properties. Crop Sci. 34:108–113. doi:10.2135/cropsci1994.0011183X003400010019x

Markhart, A.H., E.L. Fiscus, A.W. Naylor, and P.J. Kramer. 1979. Effect of temperature on water and ion transport in soybean and broccoli systems. Plant Physiol. 64:83–87. doi:10.1104/pp.64.1.83

Martin, B., and Y.R. Thorstenson. 1988. Stable carbon isotope composition (delta-C-13), water-use efficiency, and biomass productivity of *Lycopersicon esculentum*, *Lycopersicon pennellii*, and the F_1 hybrid. Plant Physiol. 88:213–217. doi:10.1104/pp.88.1.213

Mitchell, J.P., C. Shennan, S.R. Grattan, and D.M. May. 1991. Tomato fruit yields and quality under water deficit and salinity. J. Am. Soc. Hortic. Sci. 116:215–221.

Nakazato, T., D.L. Warren, and L.C. Moyle. 2010. Ecological and geographic modes of species divergence in wild tomatoes. Am. J. Bot. 97:680–693. doi:10.3732/ajb.0900216

Rick, C.M. 1976. Tomato *Lycopersicon escultentum* (Solanaceae). In: N.W. Simmonds, editor, Evolution of crop plants. Longman, London. p. 268–273.

Sinclair, T.R., and L.C. Purcell. 2005. Is a physiological perspective relevant in a 'genocentric' age? J. Exp. Bot. 56: 2777–2782. doi:10.1093/Jxb/Eri297

Torrecillas, A., C. Guillaume, J.J. Alarcon and C. Ruiz-Sanchez. 1995. Water relations of two tomato species under water stress and recovery. Plant Sci. 105: 169–176. doi:10.1016/0168-9452(94)04048-6

Truco, M.J., L.B. Randall, A.J. Bloom, and D.A. St. Clair. 2000. Detection of QTLs associated with shoot wilting and root ammonium uptake under chilling temperatures in an interspecific backcross population from *Lycopersicon esculentum* × *L. hirsutum*. Theor. Appl. Genet. 101:1082–1092. doi:10.1007/s001220051583

Wilson, J.M. 1976. Mechanism of chill-hardening and drought-hardening of *Phaseolus vulgaris* leaves. New Phytol. 76:257–270. doi:10.1111/j.1469-8137.1976.tb01459.x