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Performance of *Solanum habrochaites* LA1777 introgression line hybrids for marketable tomato fruit yield in Asia

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Abstract Wild relatives of the cultivated tomato (*Solanum lycopersicum* L.) are major sources of new genetic diversity for tomato improvement. Introgression lines (IL) are near-isogenic lines homozygous for one or several mapped wild DNA fragments in a common recurrent parent. A set of ILs developed by Cornell University from *Solanum habrochaites* accession LA1777 and recurrent parent E6203 has been made publicly available through the Tomato Genetics Resource Center of the University of California-Davis. Our objective was to identify LA1777 introgressions with potential to increase the marketable fruit yield of tomato grown in the tropics. A subset of ILs were each crossed to CLN2498E (resistant to bacterial wilt and some begomoviruses) to create IL hybrids (ILH). ILH, IL recurrent parent E6203, CLN2498E, and CLN2498E × E6203 (Hchk) were evaluated in replicated trials in Thailand, India, and Taiwan during two dry seasons. Highly significant effects for marketable fruit yield were detected in Thailand and Taiwan. ILH heterozygous for *S. habrochaites* segments at the bottom of chromosome 1 yielded about 20% than the Hchk at Thailand and Taiwan. Our results agree with previous results from Cornell University researchers who found a segment of *S. habrochaites* DNA located between TG158 and TG27 associated with increased total fruit yield in previous trials conducted in upper state New York. Yield improvement due to this *S. habrochaites* introgression can occur over a wide range of environments.

Keywords Breeding · *Lycopersicon esculentum* · *L. hirsutum* · *Solanum lycopersicum* · Wild germplasm

Abbreviations

IL	Introgression line
ILH	Introgression line hybrid

Introduction

The cultivated tomato, *Solanum lycopersicum* L. (syn. *Lycopersicon esculentum* Mill.) is the most economically important vegetable in the world (Global Horticulture Assessment 2005), grown on over four million hectares worldwide (FAO 2006)

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and an important source of vitamin A in human diets (Hanson et al. 2004). However, average tomato yields in most tropical and subtropical countries of Sub-Saharan Africa, Southeast and South Asia are relatively low and often below ten tons per hectare while average yields in temperate countries usually exceed 30 t/ha (FAO 2006). Many factors contribute to low tomato yields in the tropics, especially unadapted varieties sensitive to high temperatures and susceptible to diseases and insects. Tropically-adapted varieties with high yield potential and multiple disease resistance are a relatively cheap and effective means for small-scale farmers to substantially boost productivity, extend production in space and time, and benefit consumers by increasing vegetable supply and reducing price seasonality.

The introduction of new alleles into crops is the foundation for improvement of yield, disease resistance, quality and other characters (Simmonds 1993; Tanksley and McCouch 1997). The cultivated tomato is closely related to 13 wild *Solanum* species (Peralta et al. 2005), all of which can be crossed to tomato with varying degrees of difficulty. Highly diverse and adapted to a wide range of environments, the wild species have been a rich source of new genes for tomato improvement, particularly for disease resistance (Rick 1986). Traditional introgression of genes from wild species has been accomplished through interspecific crosses, phenotypic selection, and multiple backcrosses. Although effective for major genes conditioning qualitative traits, traditional introgression is inefficient for quantitative traits usually controlled by multiple genes. New molecular marker-based methods such as advanced backcross-QTL (Tanksley and Nelson 1996) have improved the efficiency of genetic resource exploitation and permits identification of wild alleles improving both quantitative and qualitative characters and their rapid

Table 1 Parents of introgression line hybrids (ILH) and chromosomal location of *S. habrochaites* LA1777 introgressions

Entry	♂ parent	Introgression line[a] ♀ parent	Introgression line (Cornell Code)	Introgression location[b] (chrom. no.)
ILH-1	CLN2498E	LA3913	TA1258	1
ILH-2	CLN2498E	LA3914	TA523	1
ILH-3	CLN2498E	LA3915	TA1229	1
ILH-4	CLN2498E	LA3916	TA1223	1
ILH-7	CLN2498E	LA3921	TA1105	2
ILH-17	CLN2498E	LA3933	TA1542	4
ILH-18	CLN2498E	LA3934	TA1459	4
ILH-19	CLN2498E	LA3936	TA1475	4
ILH-20	CLN2498E	LA3937	TA1473	4
ILH-21	CLN2498E	LA3938	TA1287	5
ILH-24	CLN2498E	LA3943	TA1544	5
ILH-27	CLN2498E	LA3948	TA1303	7
ILH-29	CLN2498E	LA3951	TA1312	7
ILH-37	CLN2498E	LA3962	TA1552	10, 12
ILH-38	CLN2498E	LA3964	TA1339	10
ILH-39	CLN2498E	LA3965	TA1555	2, 10,11
ILH-41	CLN2498E	LA3969	TA1121	12
ILH-42	CLN2498E	LA3970	TA1219	1
ILH-45	CLN2498E	LA3976	TA1138	1, 4
ILH-50	CLN2498E	LA3983	TA1631	5
ILH-57	CLN2498E	LA3996	TA1120	3,11
Hchk	CLN2498E	E6203	–	–
CLN2498E	–	–	–	–
E6203	–	LA4024	TA209	–

[a] Introgression lines were developed at Cornell University and assigned names with a TA prefix. The LA prefix denotes the accession number of the same introgression line at the Charles Rick Tomato Genetics Resource Center at the University of California-Davis

[b] Locations of *S. habrochaites* introgressions in LA1777 introgression lines are given in Monforte and Tanksley (2000a)

Table 2 Plot sizes, plant numbers and replication number of trials to evaluate tomato introgression line hybrids (ILH) and checks at three locations for two years in South and Southeast Asia, 2005–2006

Location	Plot size m^2		Plants/plot		Replication no.		Dates sowing/transplanting	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Taiwan	7.2 (6.0)[a]	14.4 (12.0)	12	24	2	3	15 Sep/ 15 Oct	3 Oct/ 3 Nov
Thailand	7.2 (6.0)	7.2 (6.0)	12	12	2	3	25 Oct/ 15 Nov	17Oct/ 19 Nov
India	3.6 (3.6)	7.2 (7.2)	12	24	2	4	4 Nov/ 1 Dec	6 Oct/ 17 Nov

[a] Number in parentheses is the plot area harvested for yield

Table 3 Marketable yield averaged over two years of tomato introgression line hybrids (ILH) and checks evaluated at three locations for two years in South and Southeast Asia, 2005–2006

Entry	Introgression location (chrom. no.)	AVRDC-Taiwan					TVRC-Thailand					IIHR-India[a]	
		Mean	Hchk	CLN2498	E6203	2005–2006	Mean	Hchk	CLN2498	E6203	2005–2006	Mean	2005–2006
ILH-1	1	121	**	*	**	−38	37	ns	ns	**	15	42	−32
ILH-2	1	110	ns	ns	**	−24	53	*	**	**	47	52	−33
ILH-3	1	105	ns	ns	**	−20	43	ns	*	**	20	50	−4
ILH-4	1	103	ns	ns	**	−42	39	ns	*	**	18	36	6
ILH-42	1	122	**	*	**	−50	36	ns	ns	*	24	60	−13
ILH-7	2	104	ns	ns	**	−27	37	ns	ns	**	28	51	−19
ILH-17	4	111	ns	ns	**	−38	40	ns	*	**	16	54	5
ILH-18	4	114	*	ns	**	−36	38	ns	ns	**	32	59	−5
ILH-19	4	109	ns	ns	**	−44	35	ns	ns	*	24	52	−15
ILH-20	4	104	ns	ns	**	−11	25	ns	ns	ns	21	–	–
ILH-45	1, 4	109	ns	ns	**	−12	39	ns	*	**	26	49	−29
ILH-21	5	108	ns	ns	**	−18	33	ns	ns	*	27	57	−10
ILH-24	5	111	ns	ns	**	−10	33	ns	ns	*	27	42	−11
ILH-50	5	112	*	ns	**	−23	34	ns	ns	*	20	43	−27
ILH-27	7	109	ns	ns	**	−23	22	ns	ns	ns	7	61	−23
ILH-29	7	101	ns	ns	**	−9	22	ns	ns	ns	21	52	−5
ILH-38	10	105	ns	ns	**	−46	37	ns	ns	**	33	60	−14
ILH-41	12	84	ns	**	**	−35	34	ns	ns	*	25	57	2
ILH-37	10, 12	112	*	ns	**	−15	33	ns	ns	*	11	49	12
ILH-39	2, 10,11	108	ns	ns	**	−26	39	ns	*	**	27	61	5
ILH-57	3,11	103	ns	ns	**	−23	39	ns	*	**	32	50	−32
Hchk	–	95	–	ns	**	−24	35	–	ns	*	23	52	−20
CLN2498E	–	105	ns	–	**	−14	23	ns	–	ns	−2	19	−2
E6203	–	56	**	**	–	−40	15	*	ns	–	–	–	–

[a] Mean comparisons to checks not performed due to nonsignificant entry effect

*,**, ns: Significance of mean comparison to Hchk (E6203 × CLN2498E), male parent CLN2498E, or IL recurrent parent E6203 at $P = 0.05$, $P = 0.01$, or nonsignificant, respectively

incorporation into elite cultivars by marker-assisted selection. QTLs improving tomato for total yield, solids yield, horticultural and fruit quality traits have been detected in several wild tomato species (Bernacchi et al. 1998a, b; Eshed and Zamir 1995; Eshed et al. 1994; Frary et al. 2004; Fulton et al. 1997; Fulton et al. 2000; Tanksley et al. 1996).

The development and public availability of introgression line libraries (IL) representing the systematic introgression of genetic diversity of a targeted wild tomato accession have greatly facilitated the identification and use of novel genetic variation from wild tomato species (Zamir 2001). Individual ILs contain one or a few mapped DNA fragments derived from a wild accession in the genetic background of a recurrent parent. The set of ILs is a DNA library representing up to 100% of the genome of the wild accession (Eshed and Zamir 1994, 1995; Zamir 2001). Because each IL is genetically identical to its recurrent parent except for the introgressed region, the difference in performance between an IL and its recurrent parent for a given trait can be attributed to the introgression. ILs are highly advantageous because complications arising from segregation of multiple wild genes and epistasis are avoided. Since introgressions of most ILs are relatively small, linkage drag is less problematic and horticultural characters of most IL are sufficiently acceptable so they can be evaluated in routine replicated variety trials or greenhouse experiments. Presently three IL sets for tomato are publicly available from the Tomato Genetics Resource Center at the University of California at Davis (Chetelat 2000), one from *S. pennellii* Correll (syn. *Lycopersicon pennellii* (Correll) D'Arcy) accession LA716 (Eshed et al. 1992), the second from *Solanum habrochaites* S. Knapp and D.M. Spooner (syn. *L. hirsutum* Dunal) accession LA1777 (Monforte and Tanksley 2000a), and third from *S. lycopersicoides* accession LA2951 (Canady et al. 2005); the locations and sizes of wild DNA fragments contained in individual IL along with linked markers have been published in the literature (Canady et al. 2005; Eshed and Zamir 1994; Monforte and Tanksley 2000a) and on the Solanaceae Genomics Network website (SGN 2006).

Solanum habrochaites LA1777 is a self-incompatible, green-fruited accession well known to tropical tomato breeders as a source of begomovirus and insect resistance (Momotaz et al. 2005; Monforte et al. 2001; Vidavsky and Czosnek 1998). In addition to resistance, LA1777 alleles that increase total fruit yield and brix-yield have been detected on chromosome 4 (Bernacchi et al. 1998a, b) and chromosome 1 (Monforte and Tanksley 2000b). Our objective was to evaluate selected LA1777 ILs and identify regions from LA1777 with potential to improve tomato fruit yield in the tropics and subtropics.

Materials and methods

Direct field evaluation of the LA1777 ILs for yield is difficult in tropical and subtropical Asia because E6203, the IL recurrent parent, is susceptible to bacterial wilt (caused by *Ralstonia solanacearum*) and begomoviruses, common diseases that can severely reduce yield (Fauquet et al. 2000; Hayward 1991; Morales 2001). In order to reduce the risks of disease infection, a subset of LA1777 ILs were individually crossed to CLN2498E, an AVRDC F_9 line tolerant to the bacterial wilt pathogen and carrying the *Ty*-2 allele conditioning resistance to predominant begomoviruses in Taiwan and south

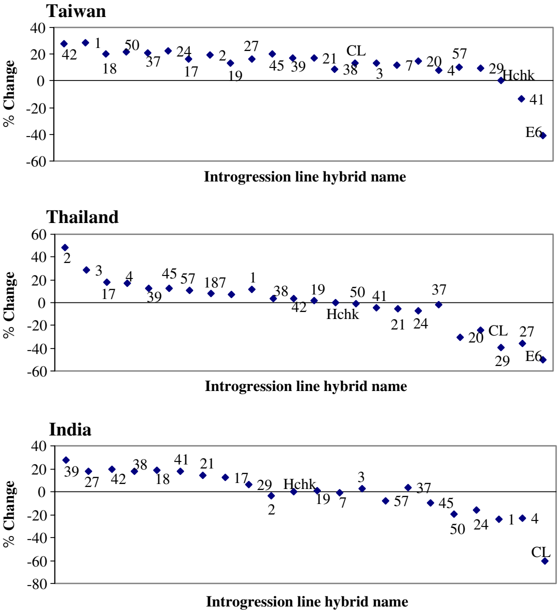

Fig. 1 Marketable yields of introgression line hybrids expressed as percentage change relative to the hybrid check (Hchk). Hchk = E6203 (IL recurrent parent) × tester line CLN2498E. The base line represents mean marketable yield (t/ha) of Hchk averaged over two years. CL = CLN2498E and E6 = E6203

India. The resulting IL hybrids (ILH) were included in field trials along with checks E6203 (recurrent parent of the IL), CLN2498E, and the F_1 of E6203 × CLN2498E (Hchk).

Field trials were conducted during the 2004–2005 (Year 1) and 2005–2006 (Year 2) dry seasons at AVRDC-the World Vegetable Center (Taiwan); the Tropical Vegetable Research Center, Kasetsart University Kamphaengsaen (Thailand); and the Indian Institute of Horticultural Research, Bangalore (India). In Year 1, entries included 64 LA1777 ILH collectively representing *S. habrochaites* introgressions from each of the 12 tomato chromosomes, and the three checks. Based on marketable fruit yield (MY) and fruit quality in Year 1, the number of ILH entries in Year 2 was reduced to 21 (Table 1). Plot sizes, and dates of sowing and transplanting for each year and location are given in Table 2. Entries were arranged in a randomized complete block design (RCBD) at all locations. Plot sizes and/or replication number were increased in Year 2, depending upon location. Plant spacing at Taiwan and Thailand was 1.5 m between rows (beds) and 40 cm between plants within rows. Plant spacing at India was 1 m between rows and 30 cm between plants within rows. Plots were harvested 2–4 times at each location. Fertilization

Table 4 Mean fruit weight (g) averaged over two years of tomato introgression line hybrids and checks evaluated at three locations for two years in South and Southeast Asia, 2005–2006

Entry	Introgression location (chrom. no.)	AVRDC-Taiwan		TVRC-Thailand					IIHR-India			
		Mean[a]	2005–2006	Mean	Hchk	CLN2498	E6203	2005–2006	Mean	Hchk	CLN2498	2005–2006
ILH-1	1	75	7	94	**	ns	**	−3	62	**	**	−14
ILH-2	1	78	22	93	**	ns	**	−1	59	**	**	−9
ILH-3	1	74	7	98	**	ns	**	−9	60	**	**	1
ILH-4	1	71	−3	89	**	*	**	−8	58	**	**	−2
ILH-42	1	72	−5	103	**	ns	**	−9	59	**	**	−8
ILH-7	2	76	3	97	**	ns	**	−10	55	*	*	−6
ILH-17	4	75	16	99	**	ns	**	−4	55	*	*	−1
ILH-18	4	81	9	98	**	ns	**	2	58	**	**	−7
ILH-19	4	76	10	91	**	*	**	−5	55	*	*	−13
ILH-20	4	79	−2	107	**	ns	**	20	–	–	–	–
ILH-45	1, 4	74	7	94	**	ns	**	−26	52	ns	ns	−3
ILH-21	5	77	1	93	**	ns	**	4	61	**	**	−19
ILH-24	5	70	9	90	**	*	**	−15	53	ns	*	6
ILH-50	5	77	5	106	**	ns	**	−6	61	**	**	−10
ILH-27	7	68	23	70	ns	**	ns	−17	49	ns	ns	−18
ILH-29	7	72	11	94	**	ns	**	−6	65	**	**	−11
ILH-38	10	70	−15	96	**	ns	**	−4	53	*	*	−12
ILH-41	12	74	12	85	**	**	**	2	54	*	*	−11
ILH-37	10, 12	71	−21	104	**	ns	**	−16	57	*	*	−10
ILH-39	2, 10, 11	65	−2	89	**	*	**	−12	52	ns	ns	−10
ILH-57	3, 11	78	4	103	**	ns	**	7	59	**	**	−8
Hchk	–	57	22	61	–	**	ns	0	42	–	ns	−19
CLN2498E	–	91	−29	107	**	–	**	−27	41	ns	–	−31
E6203	–	65	36	63	ns		–	−4	–	–	–	–

[a] Mean comparisons to checks not performed due to nonsignificant entry effect

*,**: Significance of mean comparison to Hchk (E6203 × CLN2498E), male parent CLN2498E, or IL recurrent parent E6203 at $P = 0.05$ or $P = 0.01$, respectively

and disease/insect control were performed according to local recommendations and plots were furrow-irrigated as needed.

Fruit were hand-harvested from the inner 10 or 20 plants of each plot, depending on plot size, and sorted into MY and non-marketable (cracked, insect-damaged) yield. Mean fruit size was calculated by averaging the weight of 20 random fruit from the first harvest of each plot. Fruit set was measured on 3–5 random plants per plot and percent fruit set was calculated as the (fruit number on main stem clusters 2–6) / (number of flowers on clusters 2–6) × 100. Fruit solids was measured by refractometer and estimated as Brix° (Hanson et al. 2004) and Brix°-yield (BY) was calculated as MY × (Brix°/100) (Bernacchi et al. 1998; Gur and Zamir, 2004).

Variables were subjected to analysis of variance for each year and location and over years within locations using the PROC MIXED procedure of SAS/STAT (SAS Institute 2000). For the combined analysis over years, the mixed effects model was used where year, replications, and year by entry interactions were considered random effects and entry as a fixed effect. The significance of variances associated with random effects was tested using Wald's test (Liao 2004) while significance of the entry effect was tested by *F*-test. Fischer's Protected Least Significant Difference Test was applied to determine significance of planned comparisons between the means of each ILH and the three checks.

Results

Marketable yield

Entry mean squares for individual years and over years were highly significant at Taiwan and Thailand but not India (data not shown). While entry mean squares were significant for individual years at India, the entry effect was not significant in the combined analysis. Year × entry interactions for MY were not significant at Taiwan and India, indicating that performance of entries was relatively consistent over years. A significant year × entry interaction ($P = 0.0037$) was detected in Thailand; MY of most entries were much higher in Year 1 than Year 2 and the change in magnitude of the differences among entries between years probably led to the significant interaction rather than rank changes. Because the effects for year and replications (year) are random, entry means over years can be compared in spite of the significant year × entry term (Gomez and Gomez 1984).

The MY means over years at Taiwan were relatively high, ranging from 56 t/ha to 122 t/ha (Table 3), due in part to the favorable conditions for tomato production from October to March. As expected, E6203 suffered 100% begomovirus infection at Taiwan both years, certainly a major factor accounting for its relatively low MY (56 t/ha). Begomovirus symptoms did not appear on CLN2498E and the ILH. Among checks, CLN2498E produced the highest MY (105 t/ha), followed by Hchk (95 t/ha). Over years, ILH-42 and ILH-1, both with *S. habrochaites* introgressions on chromosome 1, yielded significantly more than all three checks at Taiwan, and about 30% higher than Hchk (Fig. 1). ILH-18 and ILH-50, both with introgressions on chromosome 4, and ILH-37 with introgressions on chromosomes 10 and 12, yielded about 20% more than the Hchk.

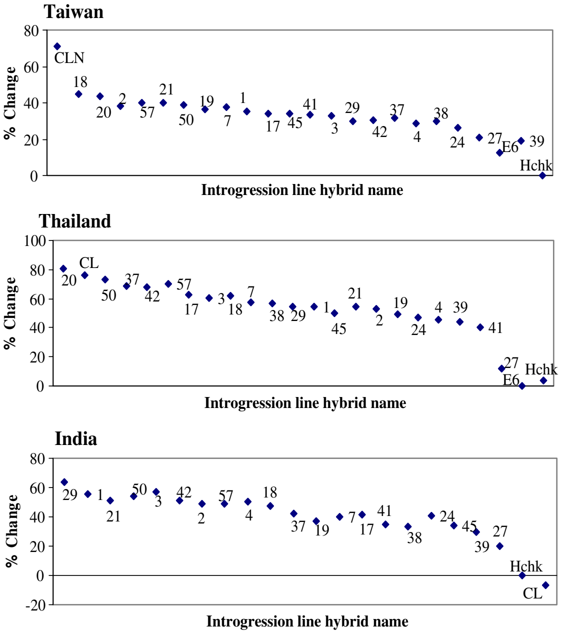

Fig. 2 Fruit weight of introgression line hybrids expressed as percentage change relative to the hybrid check (Hchk). Hchk = E6203 (IL recurrent parent) × tester line CLN2498E. The base line represents mean fruit weight (g) of Hchk averaged over two years. CL = CLN2498E and E6 = E6203

At Thailand, mean MY over entries and years was 34 t/ha and entry means ranged from 15–53 t/ha (Table 3). Begomovirus infection and relatively low fruit-set were contributing factors to the low MY of E6203 (15 t/ha) although the reason for the low MY of parental line CLN2498E (23 t/ha) is not clear. Hchk demonstrated heterosis with a MY (35 t/ha) 52% greater than its high parent, CLN2498E. ILH-2 and ILH-3, both with introgressions at the bottom of chromosome 1 yielded 51% and 23%, respectively, greater than Hchk (Fig. 1). While significant differences over years for MY were not found in the India trial, several entries such as ILH-39 and ILH-42 produced higher MY than the Hchk (Fig. 1). High yielding entries at Taiwan and Thailand such as ILH-1, ILH-2, and ILH-3 were not outstanding in India.

Fruit weight

No significant fruit weight effect for entries was detected at Taiwan. Nevertheless, mean fruit sizes of the ILHs were 8–24 g (14–42%) greater heavier than the Hchk (Table 4 and Fig. 2). At Thailand a significant entry mean square for fruit weight was found and all ILHs except ILH-27, produced significantly larger fruit than Hchk. In the India trials, 17 ILH produced significantly heavier fruit than Hchk and CLN2498E.

Fruit set

Mean fruit set of entries at Taiwan ranged from 55.5% to 76.0% (Table 5). However, the mean square over years for the fruit set effect was not significant at

Table 5 Fruit set (%) averaged over two years of tomato introgression line hybrids and checks evaluated at AVRDC-Taiwan and TVRC-Thailand, 2005–2006

Entry	Introgression location (chrom. no.)	AVRDC-Taiwan		TVRC-Thailand				
		Mean[a]	2005–2006	Mean	Hchk	CLN2498	E6203	2005–2006
ILH-1	1	75.5	−11.8	72.6	ns	*	**	−18.2
ILH-2	1	71.8	−7.2	76.0	ns	ns	**	−19.5
ILH-3	1	73.9	−8.8	70.3	ns	ns	**	−33.3
ILH-4	1	72.2	−14.5	71.3	ns	ns	**	−29.3
ILH-42	1	70.2	5.7	71.8	ns	*	**	−25.8
ILH-7	2	63.9	−5.6	70.3	ns	ns	**	−28.1
ILH-17	4	68.2	−5.2	71.4	ns	ns	**	−18.6
ILH-18	4	67.0	−12.9	70.7	ns	ns	**	−14.2
ILH-19	4	68.1	−24.7	66.9	ns	ns	**	−21.6
ILH-20	4	66.5	10.0	71.5	ns	ns	**	−17.7
ILH-45	1, 4	70.7	−7.0	66.8	ns	ns	**	−21.0
ILH-21	5	66.3	−3.7	68.0	ns	ns	**	−22.2
ILH-24	5	69.1	−16.1	64.2	*	ns	**	−17.5
ILH-50	5	68.0	−6.6	70.2	ns	ns	**	−22.8
ILH-27	7	68.8	−11.0	72.6	ns	*	**	−25.3
ILH-29	7	61.1	8.0	67.6	ns	ns	**	−25.0
ILH-38	10	62.9	−1.0	75.7	ns	**	**	−29.2
ILH-41	12	61.6	−9.6	66.8	ns	ns	**	−30.9
ILH-37	10, 12	71.2	−10.3	68.0	ns	ns	**	−19.1
ILH-39	2, 10, 11	66.0	−7.4	64.6	*	ns	**	−25.7
ILH-57	3, 11	64.9	−2.5	65.5	ns	ns	**	−28.5
Hchk	–	63.3	6.5	72.2	–	*	**	−32.6
CLN2498E	–	60.4	−0.6	63.1	*	–	*	−34.1
E6203	–	55.5	−9.2	54.6	**	*	–	−29.6

[a] Mean comparisons to checks were not performed due to a nonsignificant entry effect. Fruit set was not measured at IIHR-India both years so an analysis was not performed

*,**: Significance of mean comparison to Hchk (E6203 × CLN2498E), male parent CLN2498E, or IL recurrent parent E6203 at $P = 0.05$ or $P = 0.01$, respectively

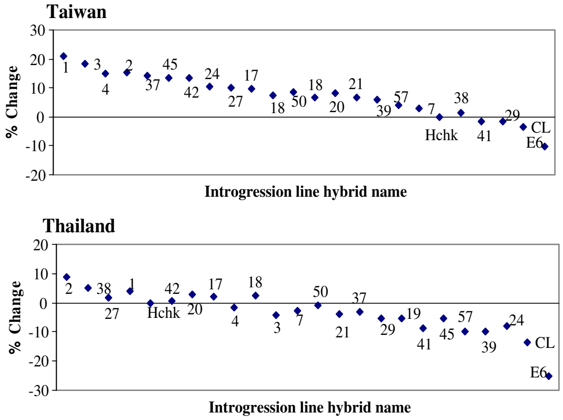

Fig. 3 Fruit-set of introgression line hybrids expressed as percentage change relative to the hybrid check (Hchk). Hchk = E6203 (IL recurrent parent) × tester line CLN2498E. The base line represents mean fruit set (%) of Hchk averaged over two years. CL = CLN2498E and E6 = E6203

Taiwan. Mean fruit set over years of most ILH were higher than the Hchk (Fig. 3) at Taiwan, especially ILH-1, ILH-3, ILH-4, and ILH-2 with introgressions on chromosome 1. At Thailand, mean fruit set of Hchk (72.2%) was significantly greater than CLN2498E and E6203; none of the ILH at the Thailand trials showed significantly higher fruit set than Hchk.

Brix°- yield

The entry mean square for the BY was not significant over years at Taiwan and mean comparisons were not performed (Table 6). At Taiwan the Hchk exhibited heterosis for BY, producing 16.9% more than its high parent, CLN2498E (Fig. 4). ILH outstanding for BY in the Taiwan trials such as ILH-1 and ILH-42 were noted earlier for their high mean MY. At Thailand, significant entry and year × entry effects for BY were detected and BY means over years of the Hchk and five ILH were significantly larger than the parental checks. ILH-2 (2.38 t/ha) and ILH-3 (1.92 t/ha) were 36% and 9.7%, respectively, higher than the Hchk (1.75 t/ha) but the differences were not significant. Significant entry effects over years were detected at the India trials for BY although none of the entries showed a significantly larger BY mean than the Hchk (2.48 t/ha). ILH-21 produced the highest BY (2.85 t/ha) in the India trials, about 15% greater than the Hchk.

Discussion

As expected, E6203 plants were infected by begomovirus at the Taiwan trials and sporadically in the India and Thailand trials. Consequently, begomovirus infection would have masked yield potential if we had attempted direct field evaluations of the susceptible ILs. Crossing each IL to a begomovirus and bacterial wilt resistant tester line like CLN2498E and evaluating the ILH avoided potential variability that would have resulted from disease infection. However, inclusion of ILH without both parents complicates interpretation of results from these trials: 1) the particular tester line may have affected expression of particular introgressions; 2) expression of beneficial recessive wild alleles would have been masked and; 3) measurement of gene action is not possible.

Over years, entries ILH-1 and ILH-42 produced significantly higher MY than the three checks at the Taiwan trials; at Thailand, only ILH-2 yielded significantly more than the checks. Four entries, ILH-1, ILH-2, ILH-3, and ILH-42, were heterozygous for overlapping *S. habrochaites* introgressions at the bottom of chromosome 1 (Fig. 5). The mean MY of these four ILH at Taiwan (115 t/ha) was 8.5% greater than the mean of the other ILH (106 t/ha), and 21% higher than the Hchk. At Thailand, the mean MY over years of these four entries (42.3 t/ha) was 23% greater than the mean of the other ILH (34.3 t/ha). Our results agree with those of Monforte and Tanksley (2000b) who by substitution mapping found a segment of *S. habrochaites* DNA located between TG158 and TG27 that increased total fruit yield. Our trials conducted in subtropical and tropical Asia and the trials of Monforte and Tanksley carried out in upper state New York indicate that this introgression can increase yield over a wide range of environments. In the New York trials, yield increases due to the wild introgression were observed most frequently in heterozygous entries (IL × E6203) and seldom in entries homozygous for the wild DNA. If this is also the case for tropical tomato varieties, it will be easier to exploit the introgression in programs targeting hybrids rather than inbred line varieties. While hybrid tomato varieties are increasingly popular in the Asia, a significant proportion of farmers in countries such as India prefer inbred line (open-pollinated) varieties (Pandey 1994).

MY is the product of fruit number per plant and average fruit weight minus the weight of unmarketable fruit. Fruit number per plant is dependent on fruit set per flower cluster and the number of flower clusters produced by each plant. Although introgressions associated with improved MY were detected at two of three locations, it was not clear which yield components were affected. In general, ILH at the Taiwan and Thailand trials showed increased fruit weight compared to Hchk as well as a slight improvement in fruit set. At Thailand (but not Taiwan), the proportion of marketable fruit to total fruit yield of ILH-1, ILH-2, ILH-3 and ILH-42 averaged about 75% compared to a mean of 65% of the other ILH (data not shown). Detailed studies to evaluate physiological processes and yield components affected by the *S. habrochaites* introgressions on chromosome 1 would improve our understanding of the reasons for increased yields. In addition to yield improvement, the region at the bottom of chromosome 1 has also been linked to some begomovirus resistance (Momotaz et al. 2005).

Table 6 Brix° yields (t/ha) averaged over two years of tomato introgression line hybrids and checks evaluated at three locations for two years in South and Southeast Asia, 2005–2006

Entry	Introgression location (chrom. no.)	AVRDC-Taiwan		TVRC-Thailand					IIHR-India			
		Mean[a]	2005–2006	Mean	Hchk	CLN2498	E6203	2005–2006	Mean	Hchk	CLN2498	2005–2006
ILH-1	1	4.92	−1.02	1.62	ns	ns	*	0.68	2.42	ns	**	−1.90
ILH-2	1	4.57	0.30	2.38	ns	**	**	2.10	2.67	ns	**	−1.96
ILH-3	1	4.28	−0.41	1.92	ns	*	**	0.57	2.58	ns	**	0.03
ILH-4	1	4.49	−0.52	1.76	ns	*	*	0.77	1.66	ns	ns	−0.13
ILH-42	1	4.77	−1.43	1.56	ns	ns	*	1.14	2.47	ns	**	−1.08
ILH-7	2	3.82	−0.62	1.59	ns	ns	*	1.07	2.19	ns	**	−1.35
ILH-17	4	4.04	−1.10	1.83	ns	*	**	0.65	2.26	ns	**	0.05
ILH-18	4	4.53	−0.09	1.63	ns	ns	*	1.00	2.67	ns	**	−0.83
ILH-19	4	4.32	−1.08	1.51	ns	ns	ns	0.86	2.80	ns	**	−1.26
ILH-20	4	4.30	0.44	1.07	*	ns	ns	0.82	–	–	–	–
ILH-45	1, 4	4.50	0.48	1.85	ns	*	**	1.28	2.15	ns	**	−1.73
ILH-21	5	4.23	−0.18	1.47	ns	ns	ns	1.22	2.85	ns	**	−1.22
ILH-24	5	4.27	0.15	1.42	ns	ns	ns	1.26	1.64	ns	ns	−0.81
ILH-50	5	4.57	−0.19	1.45	ns	ns	ns	0.81	1.72	ns	*	−1.10
ILH-27	7	3.91	−0.57	0.83	**	ns	ns	0.29	2.72	ns	**	−1.58
ILH-29	7	3.62	−0.19	1.00	*	ns	ns	1.09	2.46	ns	**	−0.54
ILH-38	10	4.02	−0.91	1.50	ns	ns	ns	1.34	2.22	ns	**	−0.57
ILH-41	12	3.19	−0.93	1.48	ns	ns	ns	1.02	2.50	ns	**	−0.70
ILH-37	10, 12	4.27	0.20	1.49	ns	ns	ns	0.72	1.77	ns	*	0.09
ILH-39	2, 10, 11	3.96	0.30	1.71	ns	*	*	1.34	2.40	ns	**	−0.91
ILH-57	3, 11	3.60	−0.47	1.66	ns	ns	*	1.28	2.62	ns	**	−2.04
Hchk	–	4.28	−1.38	1.75	–	*	*	1.07	2.48	–	**	−0.52
CLN2498E	–	3.66	0.01	1.01	*	–	ns	-0.03	0.73	**	–	−0.25
E6203	–	3.00	−2.19	0.86	*	ns	–	0.05	–	–	–	–

[a] Mean comparisons to checks not performed due to nonsignificant entry effect

Brix° estimates the fruit solids content. Brix-yield is the marketable fruit yield × (Brix° / 100) and estimates the amount of solids that could be processed into dehydrated tomato products such as paste or ketchup

[*,**] Significance of mean comparison to Hchk (E6203 × CLN2498E), male parent CLN2498E, or IL recurrent parent E6203 at $P = 0.05$ or $P = 0.01$, respectively

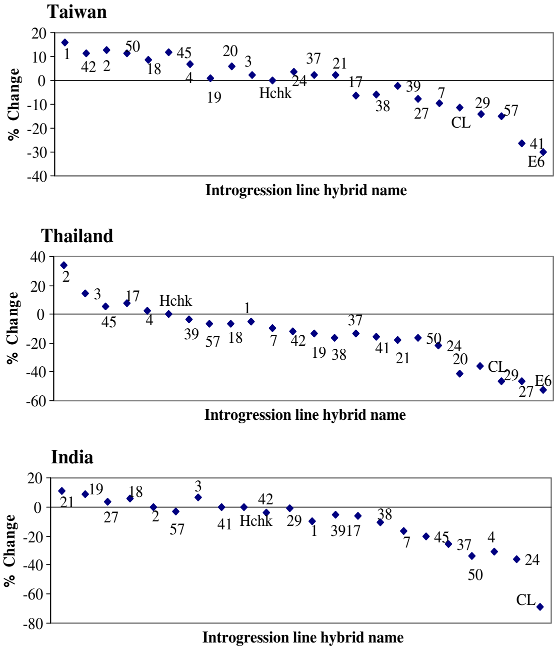

Fig. 4 Brix° yield of introgression line hybrids expressed as percentage change relative to the hybrid check (Hchk). Hchk = E6203 (IL recurrent parent) × tester line CLN2498E. The base line represents mean brix° yield (t/ha) of Hchk averaged over two years. CL = CLN2498E and E6 = E6203

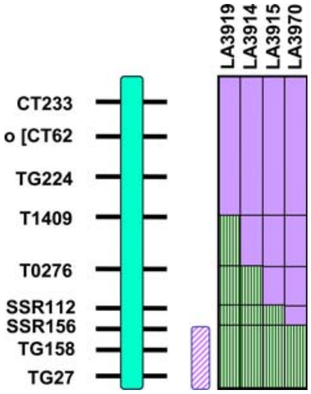

Fig. 5 Locations of *Solanum habrochaites* introgressions on chromosome 1 in four introgression lines and putative region associated with increased marketable fruit yield. RFLP and SSR markers next to the chromosome delineate introgressions in the ILs. The bar with diagonal lines to the right of the chromosome shows overlapping region containing yield enhancing genes

However, given the lack of begomovirus symptoms on most ILHs in our trials, it is unlikely that enhanced begomovirus resistance contributed appreciably to increased MY.

While ILs have limited usefulness as inbred line varieties in tropical Asia, several ILs demonstrated good potential as hybrid parents in combination with CLN2498E. Selected ILs crossed to disease resistant, tropically-adapted lines could result in commercially acceptable hybrids. For example, several ILHs in the India trial performed relatively well against current commercial hybrids (data not shown) and these ILHs will be further evaluated for their commercial potential. However, application of molecular markers to backcross targeted *S. habrochaites* regions into tropical inbred lines is the next logical step. Marker-assisted selection in populations segregating for targeted introgressions is relatively straightforward because the chromosomal location of *S. habrochaites* are published along with linked molecular markers; additional markers in targeted regions can be found in the SGN website (Solanceae Genomics Network 2006). Selection of the smallest DNA fragment containing the desired genomic region would reduce linkage drag and decrease the probability of crossover events leading to disassociation of flanking markers with the targeted alleles. LA3913, LA3914, LA3915, and LA3970 (female parents of ILH-1, ILH-2, ILH-3, and ILH-42, respectively) contain overlapping *S. habrochaites* introgressions of different sizes but all share the region around the distal part of the chromosome around TG27, the same yield-promoting region detected by Monforte and Tanksley (2000b). Among these four IL, LA3970 contains the smallest introgression. ILH-42, the hybrid of LA3970 × CLN2498E, was among the top entries at the Taiwan trials but ILH-2 carrying a larger introgression performed the best at Thailand. It is possible that LA3914 (TA523) with the larger introgression contains several yield-promoting genes. Introducing fragments of varying sizes into tropically-adapted tomato lines may be the best way to make sure all important genes are included. Once incorporated into tropical lines, it will be interesting to determine if the chromosome 1 introgression can also improve yield under more stressful conditions such as excessive moisture or drought. *S. pennellii*-derived introgressions have been associated with increased fruit yield under both drought and normal irrigation (Gur and Zamir 2004). The same authors demonstrated that pyramiding three introgressions individually associated with increased yield resulted in parental lines capable of producing hybrids yielding substantially more than leading commercial varieties (Gur and Zamir 2004). Pyramiding yield-enhancing introgressions from *S. pennellii* and *S. habrochaites* may lead to dramatic yield improvements of tropical tomato.

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