Informativeness of Single Nucleotide Polymorphisms and Relationships among Onion Populations from Important World Production Regions

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ABSTRACT. Single nucleotide polymorphisms (SNPs) were genotyped using a high-density array and DNAs from individual plants of important onion (*Allium cepa* L.) populations from major production regions and from the likely progenitor of onion, *Allium vavilovii* Popov et Vved. Genotypes at 1226 SNPs were used to estimate genetic relationships among these populations and revealed close associations among onions grown in Europe and those in North America, South America, and eastern Asia, supporting paths of introduction from Europe to the Americas and Asia. ‘Nasik Red’ is a population grown on the Indian subcontinent and was divergent from onions of European origin. Frequencies of SNPs among and within populations were used as a measure of informativeness, and 199 commonly polymorphic SNPs were identified distributed across the eight chromosomes of onion. These SNPs will be useful for estimations of relatedness among broader collections of onion populations, mapping of important phenotypes, fingerprinting of inbred lines and hybrids, and quality control of seed lots.

Onion is one of the world’s most widely grown and economically important vegetables. The likely progenitor of onion, *A. vavilovii*, grows wild in and around the Kopet Dag Mountains of Turkmenistan and Iran (Bradeen and Havey, 1995; Gurushidze et al., 2007; Hanelt, 1985; Havey, 1992; Van Raamsdonk et al., 1992). From this region, onion was introduced into the Mediterranean region. Onion cultivation subsequently spread throughout Europe; from Europe to North America, South America, Australia, sub-Saharan Africa, and New Zealand; and later from North America to Japan and eastern Asia (Goldman et al., 2001). During its worldwide dispersal, onion was selected for response to different day-length requirements for bulbing and flowering and became a biennial vegetable (Brewster, 1994). Although the length of night is important for bulbing and flowering, onion populations are classified based on the minimal daylength necessary to induce bulbing, such as short-day (≈ 12 – 13 h), intermediate-day (≈ 13 – 14 h), or long-day (>14 h) types. Production of short-day onion cultivars under longer days will produce small bulbs because of early maturation; conversely long-day cultivars grown under shorter days show little to no bulbing. Therefore, cultivars of different daylength responses may represent divergent germplasm pools within the cultivated onion.

Single nucleotide polymorphisms are robust, codominant genetic markers that commonly occur in the genomes of cultivated plants. In previous research, we completed transcriptome sequencing of onion inbreds and identified 2285 SNPs amenable for genotyping using the KASPar platform (Duangjit et al., 2013). Subsets of these SNPs were mapped in three segregating families (Damon and Havey, 2014; Duangjit et al., 2013). In this study, we genotyped 1692 of these SNPs using a high-density array and DNAs from random plants from *A. vavilovii* and 14 open-pollinated (OP) onion populations to determine how commonly polymorphisms exist in cultivated germplasm (informativeness) and to estimate relationships among the populations. We identified a set of commonly polymorphic SNPs and produced a consensus map of these SNPs across the eight chromosomes of onion.

Materials and Methods

Origins of onion populations are listed in Table 1. Doubled haploid (DH) CU066619 was included as a control to identify heterozygous SNPs (potentially from paralogous sequences) and its origin was reported by Hyde et al. (2012). DNAs were isolated using a midi-preparation (NucleoSpin Plant II kit; Macherey-Nagel, Düren, Germany) from five random plants from each of the 14 OP populations and two plants of *A. vavilovii*. DNA of DH CU066619 was isolated from pooled leaf tissue of ≈ 25 seedlings. DNA concentrations were determined spectrophotometrically and intactness by electrophoresis through 1% agarose gels.

Cytoplasm of at least 10 individual plants from each of the 14 onion populations were classified as normal (N) male-fertile or male-sterile (S) using an indel in the chloroplast accD gene

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Names are necessary to report factually on available data; however, the U.S. Department of Agriculture (USDA) neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

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Table 1. Origins, cytoplasm, and percent heterozygous loci for onion populations genotyped for 1226 single nucleotide polymorphisms (SNPs).

Population	Abbr ^z	Source ^y	Origin	Cytoplasm ^x	Het (%) ^w
Babosa	Bab	PI 257276	Spain	N	22.4
Cebolla Valenciana	Valen	PI 261591	Spain	N	26.8
Nasik Red	NasR	PI 274781	India	N	17.5
Pukekohe Longkeeper	PLK	PI 478679	New Zealand	S	25.4
Red Creole	Rcre	PI 546180	United States	N + S	26.7
Red Pinoy	Rpin	East-West Seed Co.	Philippines	N	22.5
Senshu-Ki Early	SenK	Shippo Seed Co.	Japan	N + S	30.1
Southport Yellow Globe	SYG	PI 546162	United States	N	24.3
Sweet Spanish Valencia	SSV	PI 546197	United States	N	17.8
Texas Early Grano	TEG	PI 546127	United States	N	15.5
Valcatorce	Valc	INTA	Argentina	N	19.1
White Creole	Wcre	PI 546128	United States	N + S	25.9
Wolska	Wol	PI 433343	Poland	N	27.4
Yellow Bermuda	YB	PI 546070	United States	N	26.3
<i>Allium vavilovii</i>	Avav	PI W6 19873	Turkmenistan	N	25.7

^zAbbr = abbreviation.

^yPI = PI from the USDA plant germplasm system; INTA = Instituto Nacional de Tecnología Agropecuaria and provided by C. Galmarini (Mendoza, Argentina); Shippo Seed Co. (Kagawa, Japan); East-West Seed Co. (Bangkok, Thailand).

^xCytoplasm of individual plants were classified as normal male-fertile (N) vs. male-sterile (S) as determined by the accD polymorphism (Von Kohn et al., 2013).

^wPercent heterozygosity was calculated using SNPs genotyped across five random plants from each population and two plants of *A. vavilovii*.

described by Von Kohn et al. (2013). Twenty-microliter polymerase chain reactions used primers 5'-AGAATGAGGAG-CAGGAAA and 5'-AGTCGTGATTGTTACTCTT and conditions of 50 ng of DNA, 0.25 μ M of each primer, and 5x HOT FIREPol DNA Polymerase EvaGreen HRM mix (Solis BioDyne, Tartu, Estonia). Differences in melt curves were visualized using high-resolution melting (LightCycler 480 II; Roche, Indianapolis, IN).

An Infinium array (Illumina, San Diego, CA) was constructed by Eurofins-BioDiagnostics (River Falls, WI) using 1692 SNPs (Supplemental Table 1) identified from the onion transcriptome (Duangjit et al., 2013). For array hybridizations, DNA concentrations were determined using Picogreen according to the manufacturer's instructions (Molecular Probes, Eugene, OR) and adjusted to 50 ng- μ L⁻¹. Four microliters of DNA was used for hybridization according to the Infinium HD Assay Ultra manual (Illumina). After scanning BeadChips, the raw data were analyzed using the Genome Studio genotyping module (version 2.0.3; Illumina) clustering algorithm. The auto clustering process was monitored manually and corrected when needed to produce the most accurate genotyping results. Clustering and genotype calls were proofed by a second person to eliminate any miscalling of the markers (standard protocol of Eurofins-BioDiagnostics).

Genetic distances among *A. vavilovii* and the OP onion populations were estimated using 1226 SNPs (Supplemental Table 2) and Nei's 72 coefficient of genetic diversity, and a dendrogram was generated by the unweighted paired group method algorithm (UPGMA) using Numerical Taxonomy and Multivariate Analysis System (NTSYS version 2.2; Exeter Software, Setauket, NY). Commonly polymorphic SNPs across the eight onion chromosomes were identified from a consensus map created using the JoinMap software version 4.0 (Van Ooijen, 2006) and segregations from three onion families (Damon and Havey, 2014; Duangjit et al., 2013).

Results and Discussion

Five randomly selected plants from each of 14 OP onion populations and two plants from *A. vavilovii*, and pooled DNA from seedlings of DH CU066619 were genotyped for 1692 SNPs. For the OP populations, a sample size of five plants should reveal alleles with frequencies greater than 0.25 at the 95% confidence level (Mansur et al., 1990). Two SNPs were heterozygous in DH CU066619 and were eliminated from analyses because they cannot be allelic. Of the remaining 1690 SNPs, 378 were discarded because of frequently missing genotypes and 86 discarded because they were monomorphic across all DNAs. The remaining 1226 SNPs provided genotypes across all populations (Supplemental Table 2). Overall heterozygosity averaged across the 14 OP populations was relatively low at 23.5% (Table 1). Onion shows significant

inbreeding depression (Jones and Davis, 1944) and populations are generally considered to be highly heterozygous. McCallum et al. (2008) genotyped simple sequence repeats (SSRs) using bulked DNA from onion populations and estimated median heterozygosity for OP onion populations at 70%. In contrast, Baldwin et al. (2012) isolated DNA from individual plants from diverse onion populations and reported relatively low heterozygosity at $\approx$ 22%. One explanation for the low heterozygosity revealed by this study could be the sample size of five plants per population. McCallum et al. (2008) estimated that a relatively rare allele would amplify and be detected if its frequency was greater than 5%; in our study, we would not confidently detect an allele if its frequency were less than 25%. Another explanation for the low heterozygosity observed in this study and that of Baldwin et al. (2012) may be that relatively few individuals were used during seed increases of these populations, and genetic drift may have reduced heterozygosity. However, the commercially grown cultivars Senshu-Ki Early and Red Pinoy had similar levels of estimated heterozygosity at 30.1% and 22.5%, respectively (Table 1). *Allium vavilovii*, the likely progenitor of onion (Fritsch et al., 2001; Gurushidze et al., 2007; Havey, 1992, 1997), possessed a similar level of heterozygosity at 25.7%. *Allium vavilovii* grows naturally in the Kopet Dag (Turkmen-Khorasan) mountainous region of Turkmenistan and Iran (Hanelt, 1985), and germplasm accessions may trace back to relatively few isolated plants, or bottlenecks may have occurred during seed increases of this wild species.

Plants from *A. vavilovii* and all but one of the OP populations possessed N cytoplasm as determined the accD polymorphism (Table 1). 'Pukekohe Longkeeper' (PLK) possessed only S cytoplasm as previously reported (Havey, 1993). 'Red Creole' and 'White Creole' are closely related OP populations and possessed both N and S cytoplasm. The Japanese OP population 'Senshu-Ki Early' possessed both N and S cytoplasm; this onion was likely introduced into Japan from North

Table 2. Genetic distances estimated among onion populations and *Allium vavilovii* using allele frequencies at 1226 single nucleotide polymorphisms and the Nei's 72 coefficient of genetic diversity. Larger numbers indicate greater genetic distances. Abbreviations of population names are listed in Table 1.

	Avav	Bab	NasR	PLK	Rcre	Rpin	SenK	SSV	SYG	TEG	Valc	Valen	Wcre	Wol
Bab	0.286	—												
NasR	0.262	0.251	—											
PLK	0.252	0.182	0.237	—										
Rcre	0.238	0.184	0.216	0.184	—									
Rpin	0.234	0.153	0.208	0.178	0.055	—								
SenK	0.251	0.181	0.252	0.152	0.171	0.161	—							
SSV	0.257	0.083	0.232	0.178	0.161	0.144	0.169	—						
SYG	0.268	0.226	0.249	0.176	0.202	0.204	0.166	0.202	—					
TEG	0.286	0.071	0.266	0.200	0.202	0.174	0.189	0.101	0.239	—				
Valc	0.307	0.140	0.283	0.238	0.206	0.189	0.209	0.106	0.260	0.154	—			
Valen	0.252	0.100	0.247	0.186	0.182	0.167	0.168	0.091	0.215	0.112	0.131	—		
Wcre	0.248	0.205	0.221	0.197	0.049	0.063	0.182	0.181	0.207	0.215	0.228	0.194	—	
Wol	0.279	0.216	0.297	0.194	0.221	0.210	0.190	0.225	0.190	0.243	0.289	0.218	0.232	—
YB	0.268	0.150	0.241	0.195	0.177	0.175	0.198	0.148	0.227	0.142	0.195	0.160	0.204	0.236

America, and North American OP populations can possess both cytoplasms (Havey, 1993).

Onion populations were selected as representative of key production regions or as important founder populations, and relationships were estimated using Nei's 72 coefficient of genetic diversity (Table 2) and UPGMA (Fig. 1). 'Babosa' and 'Valencia' are yellow onions originating from Spain (Goldman et al., 2001). 'Babosa' is a short-day onion producing yellow bulbs of relatively low pungency and 'Valencia' (potentially synonymous with 'Cebolla Valenciana') produces yellow bulbs with relatively good storage ability. In 1925, a population named 'Valencia Grano 9452' was introduced into the United States, initially was grown and selected in New Mexico, and eventually re-named as 'Early Grano' (Magruder et al., 1941) or 'New Mexico Early Grano' (Goldman et al., 2001). Uncertainty exists whether 'Texas Early Grano' (TEG) traces back to the 'Babosa' or 'Valencia' type. TEG has been reported to be an early-maturing selection from 'Early Grano' (Ewart, 1945) or 'Grano (Babosa)' (Perry, 1949). Bulbs of TEG are top shaped (Magruder et al., 1941) and of lower pungency, more similar to 'Babosa' than 'Valencia' types. Genotyping of SNPs revealed a close relationship between TEG and 'Babosa' (Fig. 1), supporting 'Babosa' as the origin of TEG.

'Sweet Spanish Valencia' is representative of long-day onions grown in regions of northwestern United States that produce bulbs with relatively low pungency and good storage ability. 'Sweet Spanish' onions likely trace back to introduction(s) into California and Utah from Spain in the late 1800s and early 1900s (Goldman et al., 2001; Magruder et al., 1941). Consistent with this observation, 'Sweet Spanish Valencia' was placed close to the Spanish population 'Cebolla Valenciana'. 'Valcatorce' is an important onion grown in Argentina and phenotypically similar to yellow storage onions from Spain; this OP population was placed closely to both 'Cebolla Valenciana' and 'Sweet Spanish Valencia'.

'Yellow Bermuda' was introduced from Italy (Magruder et al., 1941) into Texas via the Canary Islands in 1898 (Perry, 1949) and is the source of the male-sterile parent for 'Granex' hybrids (Goldman et al., 2001; Havey and Bark, 1994). This onion has relatively flat bulbs of low pungency that are phenotypically different from the 'Babosa' and 'Valenciana' types and grouped with onions of Spanish origin (Fig. 1).

Fig. 1. Relationships among onion populations estimated using unweighted pair group method with arithmetic mean and allele frequencies at 1226 single nucleotide polymorphisms genotyped using DNA from individual plants of each population. Abbreviated population names are listed in Table 1.

'Red Creole' and 'White Creole' are short-day onions with relatively high soluble solids and were likely introduced into southern United States from Italy (Magruder et al., 1941). 'White Creole' is an important founder population of short-day dehydrator onions in North America. 'Red Creole' and 'White Creole' are very closely related (Fig. 1), and 'White Creole' was likely selected from 'Red Creole' because it is homozygous recessive at the *C* locus (El-Shafie and Davis, 1967). 'Red Pinoy' is a pungent short-day onion grown in the Philippines and likely shares a common origin with 'Red Creole' and 'White Creole'. However, we did not detect *S* cytoplasmic plants in 'Red Pinoy' as in closely related 'Red Creole' and 'White Creole' (Table 1).

For longer day onions, 'Southport Yellow Globe' (SYG) is a well-storing onion introduced into northeastern United States from northern Europe; cultivation of this type of onion spread across northern United States and southern Canada and subsequently introduced into northern Japan and eastern Asia (Goldman et al., 2001). Consistent with this scenario is the placement of 'Early Senshu-Ki' in this long-day group. 'Pukekohe Longkeeper' from New Zealand and 'Wolska' from Poland are both well-storing, pungent, and long-day onions, and were closely related to North American onions of similar phenotypes such as SYG (Bark and Havey, 1995).

'Nasik Red' is a pungent short-day onion grown in Maharashtra state of India and was placed distantly from populations of

Table 3. Genetic map positions of single nucleotide polymorphisms (SNPs) and mean allelic frequencies across 14 onion populations and *Allium vavilovii*.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig37443_625	1	0.0	C	0.207
			G	0.793
isotig34723_664	1	3.2	C	0.530
			T	0.470
isotig37419_329	1	6.9	A	0.247
			G	0.753
isotig39789_529	1	6.9	A	0.440
			G	0.560
isotig32287_1090	1	13.2	A	0.653
			G	0.347
isotig37348_328	1	15.5	G	0.560
			T	0.440
isotig29661_1491	1	22.0	C	0.480
			T	0.520
isotig43680_368	1	24.3	G	0.307
			T	0.693
isotig37265_852	1	25.7	A	0.407
			G	0.593
isotig39274_732	1	31.9	A	0.360
			G	0.640
contig00172_269	1	36.8	A	0.607
			G	0.393
isotig26470_847	1	45.0	C	0.490
			T	0.510
isotig36938_811	1	47.6	C	0.737
			T	0.263
isotig30950_933	1	48.4	A	0.687
			G	0.313
isotig26446_844	1	51.6	C	0.482
			G	0.518
isotig32512_171	1	61.2	C	0.707
			T	0.293
isotig36337_305	1	63.6	C	0.470
			T	0.530
isotig31226_709	1	69.5	A	0.480
			G	0.520
isotig35370_364	1	69.8	A	0.900
			G	0.100
isotig29462_1710	1	70.6	C	0.700
			G	0.300
isotig29455_1102	1	70.6	A	0.590
			G	0.410
isotig32775_1170	1	70.6	A	0.687
			G	0.313
isotig31196_1500	1	71.3	C	0.987
			T	0.013
isotig27537_659	1	74.4	A	0.713
			G	0.287
isotig27517_440	1	78.0	C	0.837
			T	0.163
isotig33340_1003	1	88.6	A	0.605
			G	0.395
isotig32795_827	1	90.4	G	0.590
			T	0.410
isotig26855_718	1	96.6	A	0.653
			G	0.347
isotig21293_730	1	98.1	A	0.173

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Table 3. Continued.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig30863_958	1	108.5	G	0.827
			A	0.440
			T	0.560
isotig20159_957	1	110.0	C	0.067
			T	0.933
isotig33538_1298	2	0.0	C	0.673
			T	0.327
isotig30821_1151	2	5.3	A	0.380
			G	0.620
isotig33142_579	2	33.5	C	0.433
			T	0.567
isotig29186_1830	2	33.5	A	0.267
			G	0.733
isotig30715_1591	2	33.8	A	0.247
			G	0.753
isotig34671_610	2	34.8	A	0.460
			G	0.540
isotig33705_468	2	35.0	A	0.313
			T	0.687
isotig31346_1020	2	37.5	G	0.453
			T	0.547
isotig17237_4883	2	38.0	C	0.810
			T	0.190
isotig33533_568	2	40.0	C	0.430
			T	0.570
isotig28284_1005	2	40.4	C	0.353
			T	0.647
isotig19682_515	2	41.5	A	0.465
			G	0.535
isotig34382_910	2	54.5	C	0.393
			T	0.607
isotig15060_964	2	56.6	C	0.640
			T	0.360
isotig36775_363	2	61.4	C	0.167
			T	0.833
isotig34066_1226	2	65.6	A	0.807
			G	0.193
isotig28947_218	2	74.3	C	0.153
			T	0.847
isotig30946_1170	2	74.3	A	0.577
			G	0.423
isotig34894_810	2	75.6	A	0.303
			C	0.697
isotig33051_1252	2	75.6	C	0.560
			T	0.440
isotig32787_1241	2	85.4	A	0.187
			T	0.813
isotig36256_344	2	86.2	A	0.343
			C	0.657
isotig30461_1472	2	92.9	C	0.620
			T	0.380
isotig41662_224	2	94.3	C	0.480
			G	0.520
isotig38484_281	2	96.6	G	0.513
			T	0.487
isotig30687_1336	2	100.4	C	0.427
			T	0.573

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Table 3. Continued.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig27567_733	2	103.3	A	0.853
			G	0.147
isotig19136_223	2	104.5	A	0.927
			G	0.073
isotig40509_271	2	106.3	C	0.567
			T	0.433
isotig32390_1451	3	0.0	G	0.407
			T	0.593
isotig20406_751	3	5.7	A	0.640
			G	0.360
isotig32926_115	3	6.0	C	0.647
			T	0.353
isotig33810_581	3	7.9	C	0.540
			T	0.460
isotig18967_973	3	10.0	A	0.447
			G	0.553
isotig22876_134	3	10.4	A	0.707
			G	0.293
isotig28607_1011	3	10.7	A	0.393
			G	0.607
isotig29415_721	3	11.4	A	0.420
			G	0.580
isotig29570_2011	3	13.2	A	0.053
			G	0.947
isotig26005_1583	3	16.3	A	0.490
			G	0.510
isotig33232_1046	3	17.0	C	0.487
			T	0.513
isotig35214_301	3	17.0	A	0.480
			G	0.520
isotig27896_600	3	19.7	A	0.633
			G	0.367
isotig37687_135	3	19.7	G	0.382
			T	0.618
isotig43826_494	3	19.7	A	0.447
			G	0.553
isotig29185_1241	3	20.2	A	0.733
			G	0.267
isotig28422_1226	3	23.5	C	0.453
			T	0.547
isotig34054_350	3	23.5	A	0.387
			G	0.613
isotig35180_158	3	23.5	C	0.533
			T	0.467
isotig29460_868	3	26.3	A	0.727
			G	0.273
isotig21577_861	3	26.8	A	0.770
			C	0.230
isotig36487_789	3	26.8	A	0.277
			G	0.723
isotig42494_328	3	26.8	A	0.525
			T	0.475
isotig35352_760	3	33.1	C	0.487
			T	0.513
isotig30817_727	3	35.2	A	0.820
			C	0.180
isotig33166_330	3	49.4	C	0.587

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Table 3. Continued.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig32139_534	3	55.2	G	0.413
			C	0.517
			T	0.483
isotig31015_812	3	68.1	A	0.482
			G	0.518
isotig28347_304	3	68.9	A	0.607
			G	0.393
isotig33783_1096	3	81.1	A	0.357
			C	0.643
isotig30724_1666	3	81.2	C	0.457
			G	0.543
isotig30333_269	3	85.3	C	0.718
			T	0.282
isotig29139_1024	3	86.8	A	0.400
			G	0.600
isotig33275_395	3	88.5	A	0.443
			G	0.557
isotig33886_426	4	6.0	A	0.617
			G	0.383
isotig32333_1322	4	6.0	C	0.737
			T	0.263
isotig40309_475	4	7.2	C	0.165
			T	0.835
isotig16136_1083	4	7.2	A	0.733
			T	0.267
isotig45610_340	4	8.9	G	0.437
			T	0.563
isotig36793_769	4	11.0	C	0.470
			T	0.530
isotig28561_1513	4	15.2	C	0.060
			T	0.940
isotig37158_542	4	20.4	A	0.533
			C	0.467
isotig36493_410	4	22.2	C	0.750
			T	0.250
isotig38440_478	4	26.1	C	0.697
			T	0.303
isotig09889_661	4	28.3	C	0.203
			T	0.797
isotig26526_748	4	29.5	A	0.653
			G	0.347
isotig35268_1082	4	31.2	C	0.780
			T	0.220
isotig26045_1046	4	33.1	C	0.537
			T	0.463
isotig35345_1067	4	34.0	C	0.747
			T	0.253
isotig34783_896	4	39.3	A	0.353
			G	0.647
isotig29175_343	4	40.0	C	0.877
			T	0.123
isotig37023_265	4	40.2	A	0.600
			T	0.400
isotig33399_1211	4	40.4	A	0.603
			G	0.397
isotig19574_601	4	40.8	A	0.285
			G	0.715

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Table 3. Continued.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig32123_1465	4	42.8	A	0.380
			G	0.620
isotig28612_1057	4	45.8	A	0.173
			G	0.827
isotig37209_549	5	0.0	A	0.613
			G	0.387
isotig31278_1407	5	3.3	C	0.237
			G	0.763
isotig40014_661	5	4.6	C	0.677
			T	0.323
isotig31477_611	5	7.3	C	0.568
			T	0.432
isotig29284_408	5	7.6	A	0.203
			G	0.797
isotig28536_1567	5	30.0	A	0.087
			T	0.913
isotig28889_2528	5	31.3	C	0.673
			T	0.327
isotig33059_107	5	40.7	A	0.637
			G	0.363
isotig28803_1689	5	41.3	C	0.377
			T	0.623
isotig34069_110	5	43.3	C	0.313
			T	0.687
isotig14741_247	5	46.9	C	0.460
			T	0.540
isotig38424_376	5	50.6	A	0.160
			T	0.840
isotig34198_886	5	55.4	A	0.133
			C	0.867
isotig37670_180	5	60.0	A	0.553
			G	0.447
isotig33680_1027	5	68.3	C	0.360
			T	0.640
isotig29167_1843	5	68.4	C	0.383
			T	0.617
isotig31628_1166	5	69.1	C	0.717
			T	0.283
isotig29989_644	5	75.3	A	0.773
			G	0.227
contig00142_122	5	81.0	C	0.640
			T	0.360
isotig25097_2357	5	94.1	C	0.778
			G	0.222
isotig32307_1162	5	99.2	C	0.670
			T	0.330
isotig29293_1435	6	0.0	A	0.240
			T	0.760
isotig33019_124	6	3.0	A	0.573
			G	0.427
isotig34246_1009	6	4.2	A	0.423
			G	0.577
isotig36782_698	6	6.0	G	0.103
			T	0.897
isotig32739_152	6	6.0	C	0.247
			T	0.753
contig00298_108	6	10.4	A	0.282

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Table 3. Continued.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig28330_2105	6	22.9	G	0.718
			C	0.903
			T	0.097
isotig28451_1808	6	29.2	A	0.117
			G	0.883
isotig10023_2319	6	47.8	A	0.597
			G	0.403
isotig40098_630	6	47.8	C	0.213
			G	0.787
isotig31528_193	6	50.5	A	0.730
			G	0.270
isotig31550_508	6	50.5	A	0.657
			G	0.343
isotig30880_1388	6	51.8	A	0.563
			C	0.437
isotig35291_456	6	51.8	C	0.290
			T	0.710
isotig39121_540	6	70.2	A	0.793
			C	0.207
isotig28812_2285	6	78.7	C	0.637
			T	0.363
isotig30464_1503	6	80.8	A	0.613
			C	0.387
isotig29703_1814	6	80.8	A	0.400
			G	0.600
isotig31425_789	6	81.0	C	0.557
			T	0.443
isotig45729_183	6	81.1	C	0.677
			T	0.323
isotig33663_1163	6	82.7	C	0.883
			T	0.117
isotig38248_370	7	0.0	A	0.267
			G	0.733
isotig42387_377	7	23.5	C	0.253
			G	0.747
isotig34668_1112	7	25.2	C	0.593
			T	0.407
isotig26033_1589	7	28.6	A	0.742
			T	0.258
isotig28365_1152	7	39.6	A	0.600
			G	0.400
isotig28398_1732	7	40.9	C	0.240
			T	0.760
isotig29530_152	7	52.0	C	0.353
			T	0.647
isotig35010_835	7	56.5	A	0.403
			G	0.597
isotig28488_2757	7	57.4	C	0.907
			T	0.093
isotig26063_406	7	61.2	A	0.410
			C	0.590
isotig40501_344	7	61.3	A	0.907
			G	0.093
isotig34753_1109	7	65.8	A	0.427
			G	0.573
isotig28716_113	7	66.1	A	0.497
			G	0.503

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Table 3. Continued.

SNP	Chromosome	Genetic distance (cM)	Allele	Frequency
isotig34313_545	7	66.2	C	0.837
			T	0.163
isotig29209_2397	7	68.4	C	0.577
			T	0.423
contig00293_452	7	68.5	A	0.478
			G	0.522
isotig42645_520	7	70.6	C	0.155
			T	0.845
isotig30655_190	7	71.1	A	0.322
			C	0.678
isotig39918_357	7	73.0	C	0.717
			T	0.283
isotig33031_559	7	75.4	C	0.747
			T	0.253
isotig41937_218	7	75.5	G	0.687
			T	0.313
isotig28367_2185	8	2.9	A	0.717
			G	0.283
isotig30151_1442	8	2.9	A	0.650
			G	0.350
isotig33645_542	8	12.3	C	0.477
			T	0.523
isotig31608_1092	8	13.7	A	0.730
			G	0.270
isotig41653_558	8	30.8	C	0.460
			T	0.540
isotig37323_396	8	31.0	A	0.490
			G	0.510
isotig30323_747	8	31.0	C	0.637
			T	0.363
isotig33589_1176	8	31.0	A	0.497
			C	0.503
isotig43294_202	8	31.7	C	0.393
			T	0.607
isotig37010_277	8	31.7	C	0.210
			T	0.790
isotig32346_843	8	32.1	A	0.628
			G	0.372
isotig12913_342	8	32.8	A	0.693
			T	0.307
isotig31683_1344	8	38.4	C	0.663
			T	0.337
isotig20235_630	8	38.9	A	0.710
			G	0.290
isotig20266_1040	8	41.1	C	0.370
			T	0.630
isotig38873_388	8	44.1	C	0.170
			T	0.830
isotig30907_420	8	45.0	A	0.607
			G	0.393
isotig30020_476	8	46.8	A	0.580
			G	0.420
isotig28911_1986	8	46.9	C	0.423
			T	0.577
isotig22339_503	8	48.9	C	0.507
			T	0.493

European origin. The average Nei's 72 coefficient of genetic diversity averaged across onion populations was highest for 'Nasik Red' (0.246) and *A. vavilovii* (0.263). Baldwin et al. (2012), Khar et al. (2011), and McCallum et al. (2008) used primarily SSRs to estimate relationships among onion populations and observed that onion population(s) from the Indian subcontinent were divergent relative to onions of European origin. Together, these studies indicate that Indian onions may trace back to an independent path of introduction from central Asia and a comprehensive evaluation of onion germplasm from south Asia should be undertaken to assess genetic diversity relative to onions from Europe and related populations in the Western Hemisphere and Asia.

Genetic maps built using wide crosses may possess polymorphisms that are relatively rare in elite germplasm. We generated a consensus map (Table 3) of 199 SNPs commonly polymorphic across onion populations using segregations from three families (Damon and Havey, 2014; Duangjit et al., 2013). These SNPs are distributed across the eight chromosomes of onion and should be useful for estimation of relatedness among broader collections of onion populations, mapping of important phenotypes, fingerprinting of inbred lines and hybrids, and quality control of seed lots.

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