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

| Population          | Abbreviation | Source | Origin          | Cytoplasm* | Het (%)** |
|---------------------|--------------|--------|-----------------|------------|-----------|
| Babosa              | Bab           | PI 257276 | Spain           | N          | 22.4      |
| Cebolla Valenciana  | Val           | 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. | Poland | 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      |
| Allium vavilovii    | Avav          | PI W6 19873 | Turkmenistan | N          | 25.7      |

*Abbr = abbreviation.

**PI = 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).

+Cytoplasm 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).

+Percent 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'-AGTCGTGATTGTTAATCTCTT and conditions of 50 ng of DNA, 0.25 μM 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·μL⁻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 ≈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 cytoplasms. The Japanese OP population ‘Senshu-Ki Early’ possessed both N and S cytoplasms; this onion was likely introduced into Japan from North
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 introduction(s) of ‘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 northeastern 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 ‘Valencia’ types and grouped with onions of Spanish origin (Fig. 1).

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 | Rere | Rpin | SenK | SSV | SYG | TEG | Valc | Valen | Were | Wol |
|------|-----|------|-----|------|------|------|-----|-----|-----|------|-------|------|-----|
| Bab  | 0.286 | —    |      |      |      |      |      |      |      |      |       |      |     |
| NasR | 0.262 | 0.251| —    |      |      |      |      |      |      |      |       |      |     |
| PLK  | 0.252 | 0.182| 0.237| —    |      |      |      |      |      |      |       |      |     |
| Rere | 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|

![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.](image-url)
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     |
| isotig34723_664 | 1          | 3.2                   | G      | 0.793     |
| isotig37419_329 | 1          | 6.9                   | T      | 0.470     |
| isotig39789_529 | 1          | 6.9                   | G      | 0.753     |
| isotig32287_1090 | 1         | 13.2                  | A      | 0.247     |
| isotig37348_328 | 1          | 15.5                  | G      | 0.560     |
| isotig29661_1491 | 1         | 22.0                  | C      | 0.480     |
| isotig43680_368 | 1          | 24.3                  | T      | 0.520     |
| isotig37265_852 | 1          | 25.7                  | A      | 0.407     |
| isotig39274_732 | 1          | 31.9                  | G      | 0.593     |
| contig00172_269 | 1          | 36.8                  | A      | 0.607     |
| isotig26470_847 | 1          | 45.0                  | G      | 0.393     |
| isotig36938_811 | 1          | 47.6                  | T      | 0.510     |
| isotig30950_933 | 1          | 48.4                  | C      | 0.490     |
| isotig26446_844 | 1          | 51.6                  | T      | 0.518     |
| isotig32512_171 | 1          | 61.2                  | A      | 0.360     |
| isotig36337_305 | 1          | 63.6                  | G      | 0.640     |
| isotig31226_709 | 1          | 69.5                  | A      | 0.687     |
| isotig35370_364 | 1          | 69.8                  | G      | 0.313     |
| isotig29462_1710 | 1        | 70.6                  | G      | 0.520     |
| isotig29455_1102 | 1         | 70.6                  | A      | 0.900     |
| isotig32775_1170 | 1         | 70.6                  | A      | 0.480     |
| isotig31196_1500 | 1         | 71.3                  | G      | 0.590     |
| isotig27537_659 | 1          | 74.4                  | A      | 0.713     |
| isotig27517_440 | 1          | 78.0                  | G      | 0.287     |
| isotig33340_1003 | 1         | 88.6                  | C      | 0.837     |
| isotig32795_827 | 1          | 90.4                  | G      | 0.313     |
| isotig26855_718 | 1          | 96.6                  | A      | 0.653     |
| isotig21293_730 | 1          | 98.1                  | G      | 0.347     |

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Table 3. Continued.

| SNP            | Chromosome | Genetic distance (cM) | Allele | Frequency |
|----------------|------------|-----------------------|--------|-----------|
| isotig30863_958 | 1          | 108.5                 | A      | 0.440     |
|                |            |                       | G      | 0.827     |
| isotig20159_957 | 1          | 110.0                 | C      | 0.067     |
|                |            |                       | T      | 0.560     |
| 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     |
Table 3. Continued.

| SNP          | Chromosome | Genetic distance (cM) | Allele | Frequency |
|--------------|------------|-----------------------|--------|-----------|
| isotig27567_733 | 2          | 103.3                 | A      | 0.853     |
| isotig19136_223 | 2          | 104.5                 | A      | 0.927     |
| isotig40509_271 | 2          | 106.3                 | C      | 0.567     |
| isotig32390_1451 | 3         | 0.0                   | G      | 0.407     |
| isotig20406_751 | 3          | 5.7                   | A      | 0.640     |
| isotig32926_115 | 3          | 6.0                   | G      | 0.360     |
| isotig33810_581 | 3          | 7.9                   | C      | 0.540     |
| isotig18967_973 | 3          | 10.0                  | G      | 0.553     |
| isotig22876_134 | 3          | 10.4                  | A      | 0.707     |
| isotig28607_1011 | 3         | 10.7                  | G      | 0.393     |
| isotig29415_721 | 3          | 11.4                  | A      | 0.420     |
| isotig29570_2011 | 3         | 13.2                  | G      | 0.580     |
| isotig26005_1583 | 3         | 16.3                  | A      | 0.490     |
| isotig33232_1046 | 3         | 17.0                  | C      | 0.487     |
| isotig35214_301 | 3          | 17.0                  | G      | 0.513     |
| isotig27896_600 | 3          | 19.7                  | A      | 0.633     |
| isotig37687_135 | 3          | 19.7                  | G      | 0.367     |
| isotig43826_494 | 3          | 19.7                  | T      | 0.618     |
| isotig29185_1241 | 3         | 20.2                  | A      | 0.553     |
| isotig28422_1226 | 3         | 23.5                  | C      | 0.453     |
| isotig34054_350 | 3          | 23.5                  | T      | 0.547     |
| isotig35180_158 | 3          | 23.5                  | A      | 0.387     |
| isotig29460_868 | 3          | 26.3                  | G      | 0.613     |
| isotig21577_861 | 3          | 26.8                  | A      | 0.533     |
| isotig36487_789 | 3          | 26.8                  | G      | 0.467     |
| isotig42494_328 | 3          | 26.8                  | T      | 0.727     |
| isotig35352_760 | 3          | 33.1                  | C      | 0.273     |
| isotig30817_727 | 3          | 35.2                  | A      | 0.770     |
| isotig33166_330 | 3          | 49.4                  | C      | 0.230     |

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Table 3. Continued.

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

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| 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     |
|             |            |                       | G      | 0.778     |
| isotig25097_2357 | 5         | 94.1                  | C      | 0.222     |
|             |            |                       | T      | 0.670     |
| isotig32307_1162 | 5         | 99.2                  | C      | 0.330     |
|             |            |                       | 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     |

Continued next page
| SNP             | Chromosome | Genetic distance (cM) | Allele | Frequency |
|-----------------|------------|-----------------------|--------|-----------|
| isotig28330_2105 | 6          | 22.9                  | G      | 0.718     |
| isotig28451_1808 | 6          | 29.2                  | C      | 0.903     |
| isotig10023_2319 | 6          | 47.8                  | T      | 0.097     |
| isotig40098_630  | 6          | 47.8                  | G      | 0.883     |
| isotig31528_193  | 6          | 50.5                  | A      | 0.597     |
| isotig31550_508  | 6          | 50.5                  | G      | 0.403     |
| isotig30880_1388 | 6          | 51.8                  | C      | 0.213     |
| isotig35291_456  | 6          | 51.8                  | A      | 0.657     |
| isotig39121_540  | 6          | 70.2                  | G      | 0.343     |
| isotig28812_2285 | 6          | 78.7                  | C      | 0.437     |
| isotig30464_1503 | 6          | 80.8                  | A      | 0.290     |
| isotig29703_1814 | 6          | 80.8                  | C      | 0.207     |
| isotig31425_789  | 6          | 81.0                  | T      | 0.710     |
| isotig45729_183  | 6          | 81.1                  | A      | 0.637     |
| isotig33663_1163 | 6          | 82.7                  | G      | 0.363     |
| isotig38248_370  | 7          | 0.0                   | A      | 0.557     |
| isotig42387_377  | 7          | 23.5                  | G      | 0.267     |
| isotig43668_1112 | 7          | 25.2                  | T      | 0.323     |
| isotig26033_1589 | 7          | 28.6                  | C      | 0.443     |
| isotig28365_1152 | 7          | 39.6                  | A      | 0.613     |
| isotig28398_1732 | 7          | 40.9                  | G      | 0.437     |
| isotig29530_152  | 7          | 52.0                  | T      | 0.677     |
| isotig30010_835  | 7          | 56.5                  | A      | 0.400     |
| isotig28488_2757 | 7          | 57.4                  | G      | 0.597     |
| isotig26063_406  | 7          | 61.2                  | T      | 0.258     |
| isotig40501_344  | 7          | 61.3                  | C      | 0.400     |
| isotig34753_1109 | 7          | 65.8                  | A      | 0.427     |
| isotig28716_113  | 7          | 66.1                  | 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     |
| isotig29209_2397 | 7         | 68.4                  | C      | 0.577     |
| contig00293_452  | 7         | 68.5                  | A      | 0.478     |
| isotig42645_520  | 7         | 70.6                  | T      | 0.845     |
| isotig30655_190  | 7         | 71.1                  | T      | 0.283     |
| isotig39918_357  | 7         | 73.0                  | C      | 0.717     |
| isotig33031_559  | 7         | 75.4                  | C      | 0.747     |
| isotig41937_218  | 7         | 75.5                  | G      | 0.687     |
| isotig28367_2185 | 8         | 2.9                   | A      | 0.717     |
| isotig30151_1442 | 8         | 2.9                   | G      | 0.283     |
| isotig33645_542  | 8         | 12.3                  | C      | 0.477     |
| isotig31608_1092 | 8         | 13.7                  | G      | 0.270     |
| isotig41653_558  | 8         | 30.8                  | A      | 0.490     |
| isotig30323_747  | 8         | 31.0                  | G      | 0.510     |
| isotig33589_1176 | 8         | 31.0                  | C      | 0.637     |
| isotig43294_202  | 8         | 31.7                  | T      | 0.363     |
| isotig37010_277  | 8         | 31.7                  | A      | 0.497     |
| isotig32346_843  | 8         | 32.1                  | T      | 0.393     |
| isotig12913_342  | 8         | 32.8                  | C      | 0.693     |
| isotig31683_1344 | 8         | 38.4                  | T      | 0.307     |
| isotig20235_630  | 8         | 38.9                  | T      | 0.337     |
| isotig20266_1040 | 8         | 41.1                  | A      | 0.710     |
| isotig28911_1986 | 8         | 46.9                  | G      | 0.290     |
| isotig38873_388  | 8         | 44.1                  | C      | 0.170     |
| isotig30907_420  | 8         | 45.0                  | T      | 0.830     |
| isotig30020_476  | 8         | 46.8                  | A      | 0.607     |
| isotig22339_503  | 8         | 48.9                  | C      | 0.507     |
European origin. The average Nei’s 72 coefficient of genetic diversity averaged across onion populations was highest for ‘Nasik Red’ (0.246) and \textit{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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