Genetic Mapping of Chartreuse Bulb Color in Onion

Michael J. Havey

U.S. Department of Agriculture, Agricultural Research Service and Department of Horticulture, 1575 Linden Drive, University of Wisconsin, Madison, WI 53706

ADDITIONAL INDEX WORDS. marker-aided selection, segregation analysis, single nucleotide polymorphisms, unique vegetable color

ABSTRACT. The most common bulb colors of onion (*Allium cepa*) are red, yellow, and white; chartreuse is a relatively rare bulb color conditioned by the homozygous recessive genotype at the *G* locus. In this research, plants with chartreuse bulbs were crossed with inbreds with yellow bulbs to develop segregating families for genetic mapping of the *G* locus. For all of 17 F_2 families, segregations for yellow vs. chartreuse bulbs fit the expected 3:1 ratio ($P > 0.05$). DNAs were isolated from one F_2 family and genotyped for single nucleotide polymorphisms (SNPs) to produce a genetic map of the *G* locus and 380 SNPs, of which 119 SNPs have not been previously mapped. Segregations for yellow vs. chartreuse bulbs placed the *G* locus at the end of chromosome 7 at 6.7 cM from the nearest SNP (isotig28625_2789). This codominant SNP marker linked to the *G* locus should be useful for introgression of recessive chartreuse bulb color into diverse onion populations for commercial production of this uniquely colored onion.

The color of onion (*Allium cepa*) bulbs is one of the most important consumer traits, and bulb colors can be white, yellow, red, or chartreuse (El-Shafie and Davis, 1967). White bulbs are conditioned by a dominant allele at the inhibitor (*I*) locus or the homozygous recessive genotype at the color (*C*) locus, regardless of genotypes at other color loci. Red bulbs are conditioned by dominant alleles at all of the *C*, *R*, and *L* loci (El-Shafie and Davis, 1967). Khar et al. (2008) and Duangjit et al. (2014) described a second locus (*L2*) linked to *L* at which a dominant allele interacts with the *R* locus to condition red bulbs. Yellow bulbs have a dominant allele at *C* and the homozygous recessive genotype at one of the loci conditioning red bulbs. The *G* locus conditions “golden yellow” bulbs when the plant is *iiC-* (El-Shafie and Davis, 1967), although it is not clear how this color differs from yellow. The homozygous recessive genotype at *G* conditions chartreuse (light green) bulb color (Fig. 1) in plants that are *iiC-* regardless of genotypes at the *L* and *R* loci (El-Shafie and Davis, 1967). Chartreuse bulbs have been reported in the onion cultivars Australian Brown, Greenella, and Giza #6 (Green et al., 1997; Jones and Mann, 1963). In this research, families segregating for chartreuse bulb color were developed and the *G* locus mapped relative to SNPs. Molecular markers linked to the *G* locus should be useful for introgression of recessively inherited chartreuse bulb color into diverse onion populations.

Methods

Two plants with chartreuse bulbs were identified among progenies from the cross MSU5718A × MSU8155B, which is the female parent of the hybrid ‘Sweet Sandwich’ (Goldman et al., 2001). These two chartreuse plants were intercrossed

[breeding plot (BP) 23873]. The cytoplasm and genotype at the nuclear male-fertility restoration (*Ms*) locus (Jones and Clarke, 1943) of chartreuse plants from BP 23873 were established using pooled DNA (described subsequently) and polymorphisms in the chloroplast *accD* gene (von Kohn et al., 2013) and nuclear *AcPms1* marker (Havey and von Kohn, 2017; Kim et al., 2015), respectively. Single progenies from BP 23873 with chartreuse bulbs and waxy foliage were crossed with inbred B5351 with semiglossy foliage or inbred B9885 with glossy foliage (Damon et al., 2014). Seed was harvested separately from both parents and hybrids identified by yellow bulb color from the chartreuse parent or waxy foliage from B5351 and B9885 parents. Individual hybrid progenies were self-pollinated to produce F_2 families. Bulb colors of F_2 progenies were scored in field plots as yellow or chartreuse and goodness-of-fit to the expected 3:1 ratio was tested using chi-square analyses. Plants from one F_2 family (BP 24334) were self-pollinated and F_3 families were grown in field plots and scored for segregations of yellow vs. chartreuse bulb colors. On the basis of segregations in the F_3 families, the goodness-of-fit to the expected 1:2:1 ratio for the original F_2 family was tested using chi-square analyses.

DNA was isolated from F_2 progenies of family BP 24334 using a DNA purification kit (NucleoSpin Plant II Midi; Macherey-Nagel, Düren, Germany) and concentrations established spectrophotometrically (NanoDrop; Thermo Fisher Scientific, Waltham, MA). Single nucleotide polymorphisms (SNPs) were genotyped using DNAs from F_2 plants and the Illumina array described by Havey and Ghavami (2018). Goodness-of-fit to the expected 1:2:1 ratio for SNPs were assessed with chi-square analyses and linkages detected at a minimum linkage of logarithm of odds of 12 using Joinmap version 4 (van Ooijen, 2006). Linkage groups were assigned to chromosomes based on 160 SNPs that segregated in earlier mapping populations (Damon and Havey, 2014; Duangjit et al., 2013; Munaiz and Havey, 2020).

Results and Discussion

All of 85 progenies from the initial cross of two chartreuse plants had chartreuse bulbs, as expected because this bulb color

Received for publication 7 Nov. 2019. Accepted for publication 6 Dec. 2019.
Published online 21 January 2020.

I thank Christy Stewart and Franco Parisi for technical assistance.

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.

M.J.H. is the corresponding author. E-mail: michael.havey@usda.gov.

This is an open access article distributed under the CC BY-NC-ND license (<https://creativecommons.org/licenses/by-nc-nd/4.0/>).

Fig. 1. Chartreuse (left) vs. yellow (right four) bulb colors in onion inbred MSU5718.

Table 1. Observed segregations and probabilities of goodness-of-fit to expected 3:1 ratio for yellow vs. chartreuse (Char) bulbs in F_2 families of onion.

Cross	Observed		<i>P</i>
	Yellow	Char	
Char × B5351	115	26	0.072
	86	29	0.957
	34	9	0.538
B5351 × Char	53	21	0.502
	54	17	0.837
	58	29	0.073
	41	15	0.758
	48	19	0.526
B9885 × Char	104	34	0.922
	107	31	0.491
	98	22	0.092
	105	31	0.552
Char × B9885	85	31	0.668
	98	23	0.128
	71	33	0.113
	101	32	0.802
	114	43	0.489

is conditioned by the homozygous recessive genotype at the *G* locus (El-Shafie and Davis, 1967). Polymorphisms in chloroplast *accD* (von Kohn et al., 2013) and nuclear *AcPms1* marker (Havey and von Kohn, 2017; Kim et al., 2015) established that the chartreuse plants selected in this study were S cytoplasmic and possessed dominant alleles at the *Ms* locus, indicating that the original chartreuse plants likely originated from self-pollination within cytoplasmic male-sterile line MSU5718A due to the presence of male-fertility restoration allele(s) at the *Ms* (Jones and Clarke, 1943).

Segregations of yellow vs. chartreuse bulbs fit the expected 3:1 ratio for all of 17 F_2 families from crosses of chartreuse plants with inbreds B5351 and B9885 (Table 1), in agreement with the genetic model proposed by El-Shafie and Davis (1967). For F_3 families from the cross of a chartreuse plant with B5351, 22 families had only chartreuse bulbs, 46 segregated for chartreuse and yellow bulbs, and 15 families had

only yellow bulbs which fit the expected 1:2:1 segregation [$P = 0.340$ (Table 2)]. A total of 1624 SNPs (Havey and Ghavami, 2018) were genotyped using DNAs from 92 F_2 progenies, of which 380 segregated and all fit the expected 1:2:1 ratio at $P > 0.01$ (Table 2). The map locations of 119 previously unmapped SNPs were established (indicated with bold text in Table 2). It was surprising that segregations for bulb colors (Table 1) and all SNPs (Table 2) fit the expected segregation ratios, which may have resulted in parents well adapted to growing conditions in Wisconsin and the robustness of SNP genotyping using the Illumina platform and DNAs from individual plants.

The *G* locus mapped to the end of chromosome 7 at 6.7 cM distal from SNP isotig28625_2789 (Table 2). Other major loci conditioning bulb colors in onion have been mapped; the *C* locus maps to chromosome 6, *L* and *L2* to chromosome 4, and *G* and *R* to chromosome 7 (Khar et al., 2008; Masuzaki et al., 2006) (Table 2). The *I* locus showed linkage at 21 cM with ACM006 (Khar et al., 2008), a simple sequence repeat which has not been placed on the genetic map of onion. Khar et al. (2008) reported that the candidate gene for the *R* locus [dihydroflavonol 4-reductase (Kim et al., 2004)] mapped 11.1 cM from a restriction fragment length polymorphism revealed by clone AOB212 (King et al., 1998) on chromosome 7. In the genetic map developed by Duangjit et al. (2013), AOB212 mapped 11.2 cM from SNP isotig37252_318 and 27.4 cM from isotig25801_1760. Both of these SNPs segregated in the chartreuse × B5351 map (Table 2), and comparison of these marker positions and orientations indicate that the *G* locus should map ≈12 cM from *R* on chromosome 7.

The colors of vegetables impact consumer acceptance, and consumers may respond positively to uniquely colored vegetables as long as other sensorial characteristics (e.g., flavor, texture, aroma) are acceptable (Leksrisompong et al., 2012). Chartreuse onions rarely appear in markets and may be attractive to consumers interested in uniquely colored vegetables. The SNP marker linked with the *G* locus on chromosome 7 should be useful for backcrossing recessively inherited chartreuse bulb color into elite onion populations, avoiding the need to self-pollinate after each backcross generation to identify heterozygotes and expediting commercial production of onions with this unique bulb color.

Table 2. Chromosome (Chrom), position in centiMorgans, observed (Obs) segregations, and probabilities of goodness-of-fit to expected 1:2:1 ratios for single nucleotide polymorphisms (SNPs) and chartreuse vs. yellow bulb colors in an F₂ family of onion.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			P
			a	h	b	
isotig36152_175	1	0.0	20	40	23	0.850
isotig36152_520	1	0.0	20	37	23	0.714
isotig36152_541	1	0.0	20	39	23	0.813
isotig36152_724	1	0.0	20	40	23	0.850
isotig26855_718	1	15.2	23	34	22	0.459
isotig14997_1521	1	22.8	21	43	19	0.903
isotig33254_1237	1	22.8	21	43	19	0.903
isotig33254_614	1	22.8	21	43	19	0.903
isotig33340_1003_Z	1	29.9	22	46	15	0.340
isotig33340_203_Z	1	29.9	22	46	15	0.340
isotig33340_887_Z	1	29.9	22	45	15	0.372
contig13740_1338	1	32.5	21	46	16	0.454
isotig31711_748_Z	1	43.1	24	46	13	0.143
isotig32282_1109_Z	1	43.7	24	45	14	0.223
isotig32282_834_Z	1	43.7	24	45	14	0.223
isotig30097_102_Z	1	48.8	24	45	14	0.223
isotig27517_440	1	51.3	25	45	13	0.131
isotig21900_461	1	51.5	25	41	13	0.153
isotig12342_956	1	51.9	25	44	14	0.200
isotig29462_1710	1	51.9	25	44	14	0.200
isotig32775_1170	1	51.9	25	43	14	0.207
isotig34700_979	1	51.9	25	44	14	0.200
isotig35370_364	1	51.9	25	44	14	0.200
isotig30684_1001	1	52.5	25	45	13	0.131
isotig31577_1041	1	52.5	25	45	13	0.131
isotig31577_1144	1	52.5	25	45	13	0.131
isotig37136_342	1	52.5	25	43	13	0.145
isotig37136_916	1	52.5	25	45	13	0.131
isotig29923_361	1	53.1	24	46	13	0.143
isotig26470_847	1	59.5	23	41	18	0.737
isotig26470_916	1	59.5	23	42	18	0.735
isotig32772_1128	1	60.7	22	42	19	0.892
isotig32772_1413	1	60.7	22	41	19	0.896
isotig32772_993	1	60.7	22	42	19	0.892
isotig39326_587	1	62.0	21	42	20	0.982
isotig34779_398	1	62.6	22	41	20	0.947
isotig36532_814	1	62.6	22	41	20	0.947
isotig33710_284	1	67.6	22	41	20	0.947
isotig33710_856	1	67.6	22	41	20	0.947
isotig32235_511	1	70.1	22	39	22	0.860
isotig32235_925	1	70.1	22	39	22	0.860
isotig30917_789	1	72.6	22	39	22	0.860
isotig39274_732	1	72.6	22	39	22	0.860
isotig33099_885	1	75.2	24	34	23	0.348
isotig43680_368	1	85.9	25	34	23	0.288
isotig44346_390	1	87.8	27	33	22	0.155
isotig40122_430	1	90.4	22	36	23	0.599
isotig18286_1848	1	98.8	18	43	22	0.781
isotig37348_328	1	101.3	19	42	21	0.929
isotig32466_361	1	101.9	20	41	21	0.988
contig00534_1173	1	107.7	19	40	23	0.803
contig00534_1431	1	107.7	19	41	23	0.820
contig00534_1708	1	107.7	19	41	23	0.820
isotig32287_1090	1	107.7	19	41	23	0.820
isotig32674_652	1	107.7	19	41	23	0.820
isotig35260_950	1	107.7	19	40	23	0.803

Continued next page

Table 2. Continued.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			P
			a	h	b	
isotig38094_540	1	111.5	20	39	22	0.900
isotig37443_625	1	115.4	17	44	21	0.661
isotig32416_877_Z	2	0.0	21	37	23	0.703
isotig31747_650_Z	2	11.7	21	36	22	0.724
isotig31512_171_Z	2	12.3	21	41	21	0.994
isotig22791_480	2	14.8	21	39	23	0.820
contig00172_336	2	19.2	18	42	23	0.735
isotig30979_1313	2	19.2	18	42	23	0.735
isotig30979_525	2	19.2	18	42	23	0.735
isotig35870_429	2	19.2	18	42	23	0.735
isotig35870_603	2	19.2	18	42	23	0.735
contig00087_991	2	21.0	15	42	23	0.407
isotig09466_645	2	21.0	15	45	23	0.344
isotig09466_656	2	21.0	15	44	23	0.368
isotig28648_1787	2	21.0	15	45	23	0.344
isotig28648_2282	2	21.0	15	45	23	0.344
isotig28648_659	2	21.0	15	45	23	0.344
isotig29186_1830	2	21.0	15	42	23	0.407
isotig29645_1947	2	21.0	15	45	23	0.344
isotig30856_1351	2	21.0	15	41	23	0.420
isotig30856_1616	2	21.0	15	39	23	0.433
isotig32987_1114	2	21.0	15	42	23	0.407
isotig32987_979	2	21.0	15	41	23	0.420
isotig33142_579	2	21.0	15	45	23	0.344
isotig37633_597	2	21.0	15	45	23	0.344
isotig17237_4883_Z	2	21.6	15	42	22	0.459
isotig19682_515	2	21.6	15	46	22	0.340
isotig25181_1307	2	21.6	15	43	22	0.433
isotig33006_887	2	21.6	15	46	22	0.340
isotig40415_434	2	25.4	16	46	21	0.454
isotig33652_1174	2	26.0	16	45	22	0.482
isotig42036_531	2	26.7	15	40	22	0.499
isotig39285_573	2	33.3	19	46	18	0.607
isotig15060_964	2	33.9	19	44	19	0.803
isotig31233_1053_Z	2	33.9	19	39	19	0.994
isotig36775_363_Z	2	35.8	18	48	17	0.357
isotig34497_853	2	42.3	24	42	15	0.348
isotig31728_1335	2	43.0	24	45	14	0.223
isotig33627_701	3	0.0	31	32	20	0.026
isotig32949_1359	3	1.2	32	32	19	0.015
isotig32926_115	3	7.8	30	34	19	0.060
isotig34825_1197	3	9.1	29	34	20	0.097
isotig18967_973	3	12.2	31	33	19	0.031
isotig34535_1112	3	14.0	29	35	18	0.095
isotig29415_721	3	14.1	29	36	18	0.112
isotig29570_2011	3	14.7	29	35	19	0.108
isotig31763_1091_Z	3	17.8	27	38	18	0.281
isotig31763_1363_Z	3	17.8	27	38	18	0.281
isotig31763_1594_Z	3	17.8	27	36	18	0.223
isotig31763_874_Z	3	17.8	27	37	18	0.252
isotig31763_961_Z	3	17.8	27	38	18	0.281
isotig31999_483	3	17.8	27	38	18	0.281
isotig32200_317_Z	3	19.6	27	39	17	0.258
isotig32041_963	3	20.2	26	40	17	0.357
isotig33232_1046	3	20.2	26	40	17	0.357
isotig33232_1240	3	20.2	26	40	17	0.357

Continued next page

Table 2. Continued.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			P
			a	h	b	
isotig33232_163	3	20.2	26	40	17	0.357
isotig35214_710	3	20.2	26	40	17	0.357
isotig19473_316	3	20.8	26	39	18	0.398
isotig30363_1184	3	21.4	26	38	19	0.412
isotig30363_1478	3	21.4	26	38	19	0.412
isotig30363_1650	3	21.4	26	38	19	0.412
isotig30453_1365	3	21.4	26	38	19	0.412
isotig27896_600	3	22.0	26	39	18	0.398
isotig25849_1264	3	22.6	26	40	17	0.357
isotig25849_1265	3	22.6	26	40	17	0.357
isotig32768_708	3	22.6	26	40	17	0.357
isotig29185_1241	3	24.5	26	41	16	0.298
isotig29185_1803	3	24.5	26	41	16	0.298
isotig29185_2039	3	24.5	26	41	16	0.298
isotig34830_369	3	26.3	28	38	17	0.173
isotig33431_426	3	27.5	29	36	18	0.112
isotig16345_1175	3	31.9	28	37	18	0.184
isotig35180_158	3	31.9	28	37	18	0.184
isotig28422_1511	3	32.6	28	36	19	0.182
isotig28422_191	3	32.6	28	36	19	0.182
isotig34054_350	3	32.6	28	36	19	0.182
isotig31657_1599	3	39.0	25	40	18	0.525
isotig29736_2072_Z	3	42.8	26	40	17	0.357
isotig25719_1531_Z	3	44.6	23	43	17	0.614
isotig35352_760_Z	3	45.3	23	42	18	0.735
isotig35663_382	3	45.9	23	41	19	0.820
isotig35663_432_Z	3	45.9	23	37	18	0.655
isotig20004_416	3	50.9	26	35	22	0.298
isotig29785_1760	3	52.1	26	37	20	0.398
isotig30958_160	3	52.1	26	37	20	0.398
isotig33166_330	3	52.1	26	37	20	0.398
isotig34107_268	3	52.1	26	37	20	0.398
isotig34107_828	3	52.1	26	37	20	0.398
isotig35740_1032	3	52.1	24	37	20	0.607
isotig35740_296	3	52.1	26	37	20	0.398
isotig35740_662	3	52.1	26	37	20	0.398
isotig32139_534	3	55.3	25	36	22	0.433
isotig42601_220	3	55.3	25	34	22	0.315
isotig33343_325	3	61.7	23	36	24	0.477
isotig35038_614	3	62.3	22	31	24	0.220
isotig15391_778	3	73.0	23	37	23	0.614
isotig15391_917	3	73.0	23	36	23	0.543
isotig29611_2140	3	77.4	23	36	24	0.477
isotig30944_607	3	77.4	23	36	24	0.477
isotig31416_1679	3	77.4	23	36	24	0.477
isotig35014_773	3	77.4	23	34	24	0.348
isotig33256_667_Z	3	78.0	23	37	23	0.614
isotig31068_1490	3	78.7	22	36	22	0.670
isotig32617_1476_Z	3	79.9	21	38	24	0.668
isotig33783_1096	3	87.0	23	36	22	0.599
isotig32564_718	3	87.6	22	38	23	0.735
isotig29139_1024	3	91.4	23	36	24	0.477
isotig29139_1381	3	91.4	20	40	23	0.850
isotig29139_1610	3	91.4	20	40	23	0.850
isotig29139_382	3	91.4	20	40	23	0.850
isotig29139_508	3	91.4	20	40	23	0.850

Continued next page

Table 2. Continued.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			P
			a	h	b	
isotig29139_510	3	91.4	20	40	23	0.850
isotig29680_725	3	92.0	21	39	23	0.820
isotig29251_1141	3	92.6	20	36	23	0.654
isotig29251_1827	3	92.6	20	40	23	0.850
isotig29251_631	3	92.6	20	40	23	0.850
isotig26975_1187	3	95.1	21	40	22	0.936
isotig35099_237_Z	3	96.1	19	40	22	0.889
isotig16559_476	3	98.2	19	41	23	0.820
isotig36605_668	4	0.0	20	43	20	0.947
isotig19074_908	4	0.6	20	41	21	0.988
isotig28762_702	4	3.4	20	42	21	0.982
isotig19902_1219	4	5.4	17	42	21	0.741
isotig19902_637	4	5.4	19	43	21	0.903
isotig31547_1040	4	7.2	18	44	21	0.772
isotig31547_1204	4	7.2	18	44	21	0.772
isotig31547_1238	4	7.2	18	44	21	0.772
isotig31547_938	4	7.2	17	44	21	0.661
isotig33497_721_Z	4	11.0	16	44	23	0.477
isotig37158_542	4	14.1	15	47	21	0.313
contig00010_596	4	15.3	16	44	22	0.518
isotig28878_757	4	15.3	16	45	22	0.482
isotig30201_786	4	15.3	16	44	22	0.518
isotig26526_748_Z	4	15.9	16	43	23	0.499
isotig26526_995_Z	4	15.9	16	43	23	0.499
isotig32504_1288	4	15.9	16	41	23	0.529
isotig37005_693	4	16.2	15	43	23	0.389
isotig20995_770	4	16.5	15	40	23	0.429
isotig28741_496	4	16.5	15	45	22	0.372
isotig31736_1067_Z	4	16.5	15	45	23	0.344
isotig37005_723	4	16.5	15	45	23	0.344
isotig32123_1465	4	17.7	14	45	24	0.223
isotig37023_265	4	18.3	14	46	23	0.231
isotig33399_1211	4	18.9	14	45	24	0.223
isotig33399_848	4	18.9	14	45	24	0.223
isotig38732_575_Z	4	18.9	13	45	24	0.155
isotig37385_830	4	21.4	11	49	23	0.045
isotig44683_192	4	23.9	10	47	23	0.036
isotig44683_264	4	23.9	11	49	23	0.045
isotig31392_1426_Z	4	27.0	12	47	23	0.095
isotig35268_1082_Z	4	27.0	12	48	21	0.092
isotig35268_784_Z	4	27.0	12	48	23	0.084
isotig35268_979_Z	4	27.0	12	48	23	0.084
isotig21411_854	4	27.6	12	47	24	0.085
isotig21411_971	4	27.6	12	47	24	0.085
isotig33429_1166	4	28.8	13	47	23	0.145
isotig34748_190	4	30.7	13	48	22	0.136
isotig29269_1573	4	37.8	11	51	21	0.034
isotig36493_410	4	38.4	11	51	20	0.032
isotig31300_1079	4	39.0	12	50	20	0.064
isotig41344_259_Z	4	39.0	12	50	20	0.064
isotig41344_432_Z	4	39.0	12	50	20	0.064
isotig31846_429	4	39.6	12	49	21	0.078
isotig41409_219	4	50.4	18	42	23	0.735
isotig37821_673	4	54.2	17	43	22	0.669
isotig16136_1083	4	57.9	19	44	20	0.850
isotig16136_752	4	57.9	19	44	20	0.850

Continued next page

Table 2. Continued.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			P
			a	h	b	
isotig16136_978	4	57.9	19	44	20	0.850
isotig16136_983	4	57.9	19	44	20	0.850
isotig31663_1466	4	57.9	19	44	20	0.850
isotig33886_426	4	61.8	20	45	14	0.295
isotig27765_337	4	66.3	20	45	18	0.709
isotig31106_505	4	68.8	20	47	16	0.398
isotig32888_1192	5	0.0	21	46	16	0.454
isotig26546_969	5	9.7	20	44	19	0.850
isotig28889_2528	5	17.9	20	38	25	0.551
isotig30732_1102	5	17.9	20	38	25	0.551
isotig30732_1647	5	17.9	20	37	22	0.812
isotig33784_560	5	17.9	20	38	25	0.551
isotig17421_2154	5	23.6	17	43	23	0.614
isotig30429_128	5	23.6	17	43	23	0.614
isotig33059_107	5	25.5	17	44	22	0.636
isotig34069_110	5	26.1	16	45	22	0.482
isotig25217_2228	5	27.3	15	45	23	0.344
isotig14741_247_Z	5	27.9	15	46	22	0.340
isotig34198_886	5	29.1	14	43	23	0.290
isotig38424_376	5	29.1	14	46	23	0.231
isotig38424_472	5	29.1	14	46	23	0.231
isotig35819_544_Z	5	30.4	12	48	23	0.084
isotig37670_180	5	31.6	10	50	23	0.023
isotig32130_277	5	33.4	11	49	23	0.045
isotig35125_448	5	34.0	11	46	23	0.067
isotig30202_736	5	35.3	11	50	21	0.041
isotig30202_796	5	35.3	11	50	22	0.041
isotig30202_919	5	35.3	11	50	21	0.041
isotig32901_1407	5	35.9	11	49	21	0.049
isotig34751_952	5	35.9	11	51	21	0.034
isotig29818_190_Z	5	36.5	11	45	22	0.084
isotig29818_808_Z	5	36.5	11	50	22	0.041
isotig31385_287_Z	5	37.1	10	51	22	0.020
isotig32805_1160	5	39.6	10	51	22	0.020
isotig37875_830	5	42.7	11	47	22	0.065
isotig31152_1676	5	44.5	12	50	20	0.064
isotig38068_242	5	44.5	12	51	20	0.053
isotig06563_373	6	0.0	18	46	18	0.543
isotig31615_250	6	0.0	18	47	18	0.482
isotig34246_1009	6	0.0	18	44	18	0.670
isotig32739_152	6	1.8	20	45	17	0.607
isotig32739_439	6	1.8	20	46	17	0.551
isotig36782_698	6	1.8	18	43	17	0.655
isotig36295_652_Z	6	3.1	21	44	16	0.543
isotig28330_2105	6	7.5	20	47	16	0.398
isotig29848_1923	6	7.5	20	46	16	0.447
isotig30657_998	6	7.5	20	47	16	0.398
isotig20052_1261	6	11.2	21	45	17	0.614
isotig31703_857	6	11.2	21	45	17	0.614
isotig32152_614	6	13.1	18	47	16	0.335
isotig31280_1328	6	23.8	21	44	18	0.772
isotig31280_1391	6	23.8	21	44	18	0.772
isotig31280_1610	6	23.8	21	44	18	0.772
isotig35768_1013	6	25.0	21	44	18	0.772
isotig28527_2500	6	28.8	22	42	17	0.695
isotig32066_1149	6	30.6	22	43	18	0.781

Continued next page

Table 2. Continued.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			P
			a	h	b	
isotig32066_1385	6	30.6	22	43	18	0.781
isotig32066_515	6	30.6	22	43	18	0.781
isotig32066_821	6	30.6	22	42	18	0.803
isotig10023_2319	6	34.4	20	41	20	0.994
isotig31550_508_Z	6	40.2	22	37	21	0.789
isotig31550_658_Z	6	40.2	22	39	21	0.896
isotig31550_670_Z	6	40.2	22	40	21	0.936
isotig16577_681	6	42.4	19	43	21	0.903
isotig28276_1535	6	46.5	20	42	21	0.982
isotig28276_320	6	46.5	20	42	21	0.982
isotig30163_1380	6	47.7	19	44	20	0.850
isotig35291_456	6	50.8	16	44	19	0.534
isotig34877_391	6	60.9	17	46	20	0.551
isotig35250_340	6	62.1	16	48	19	0.324
isotig30463_150	6	64.6	15	46	22	0.340
isotig30463_249	6	64.6	15	46	22	0.340
isotig28768_2758	6	65.8	15	46	22	0.340
isotig30686_364	6	70.9	15	48	20	0.267
isotig30686_371	6	70.9	14	46	20	0.259
isotig30686_719	6	70.9	15	48	20	0.267
isotig31045_384_Z	6	70.9	15	48	20	0.267
isotig26300_278	6	78.0	17	45	21	0.614
isotig36354_189	6	78.0	17	42	21	0.741
isotig29703_1814	6	86.5	18	44	21	0.772
isotig30292_771	6	86.5	18	43	21	0.813
isotig30464_1503	6	86.5	18	44	21	0.772
isotig30464_1566	6	86.5	18	44	21	0.772
isotig30464_804	6	86.5	18	44	21	0.772
isotig31266_1737	6	86.5	18	44	21	0.772
isotig31266_696	6	86.5	18	44	21	0.772
isotig31266_752	6	86.5	18	44	21	0.772
isotig33111_603	6	86.5	18	44	21	0.772
isotig45729_183	6	86.5	18	44	21	0.772
isotig37324_542	6	90.3	15	46	18	0.306
isotig30426_1109	6	94.9	18	47	18	0.482
isotig38248_370	7	0.0	18	45	18	0.607
isotig35721_667_Z	7	2.6	21	44	18	0.772
isotig42233_514_Z	7	12.5	18	44	21	0.772
isotig32031_755	7	18.2	18	45	20	0.709
isotig29081_692	7	25.3	19	40	20	0.981
isotig29157_1045	7	32.4	15	50	18	0.157
isotig29157_1114	7	32.4	15	50	18	0.157
isotig29157_1276	7	32.4	15	49	18	0.188
isotig29157_1297	7	32.4	15	50	18	0.157
isotig29157_1381	7	32.4	15	50	18	0.157
isotig36575_674	7	32.4	16	49	18	0.246
isotig36575_914	7	32.4	16	46	18	0.387
isotig42387_377	7	34.2	17	47	19	0.460
isotig34668_1112_Z	7	35.5	19	45	19	0.744
isotig26033_1589	7	37.3	19	44	20	0.850
isotig26033_878	7	37.3	19	40	20	0.981
isotig30642_156_Z	7	37.3	20	42	19	0.934
isotig28418_576	7	38.6	19	43	20	0.896
isotig29101_440	7	41.7	19	43	21	0.903
isotig29101_970	7	41.7	19	43	21	0.903
isotig30182_1370	7	41.7	19	43	21	0.903

Continued next page

Table 2. Continued.

SNP or locus ^z	Chrom no.	Position (cM)	Observed ^y			<i>P</i>
			a	h	b	
isotig35377_1073	7	41.7	19	43	21	0.903
isotig26063_757	7	42.3	19	42	22	0.892
isotig28716_2573	7	49.7	22	40	20	0.929
contig00293_452_Z	7	52.2	22	41	20	0.947
isotig33385_137	7	52.8	21	42	20	0.982
isotig33385_293_Z	7	52.8	21	42	20	0.982
isotig33385_518_Z	7	52.8	21	42	20	0.982
isotig36956_785	7	52.8	21	36	20	0.839
isotig25801_1760_Z	7	56.0	22	41	20	0.947
isotig28956_1195	7	56.0	22	41	20	0.947
isotig30655_190	7	56.0	22	41	20	0.947
isotig37252_318	7	63.4	21	44	18	0.772
isotig38160_373	7	71.5	24	38	21	0.668
isotig28625_2789	7	79.6	22	42	19	0.892
<i>G</i> locus	7	86.3	22	46	15	0.340
isotig37101_618	8	0.0	22	40	19	0.889
isotig27349_313	8	4.3	20	40	20	1.000
isotig34435_676	8	8.6	19	45	19	0.744
isotig34435_689	8	8.6	19	42	19	0.905
isotig30047_888	8	12.3	16	43	22	0.549
isotig30104_1528	8	12.3	16	45	22	0.482
isotig29442_1161_Z	8	17.4	14	45	24	0.223
isotig28373_3204	8	26.7	15	41	27	0.175
isotig28373_866	8	26.7	15	40	27	0.169
isotig28412_1084_Z	8	30.5	14	41	28	0.094
isotig28412_1177_Z	8	30.5	14	41	28	0.094
isotig33362_1094_Z	8	31.7	15	41	27	0.175
isotig12913_342	8	33.5	16	42	25	0.375
isotig28432_1209	8	35.4	16	41	26	0.298
isotig28432_1302	8	35.4	16	40	26	0.288
isotig37010_277	8	35.4	16	37	26	0.241
isotig37010_673	8	35.4	16	41	26	0.298
isotig43294_202_Z	8	35.4	16	41	26	0.298
isotig37323_396	8	41.2	17	36	27	0.192
isotig20266_1040	8	53.5	15	41	26	0.229
isotig20266_541	8	53.5	15	42	26	0.231
isotig30907_420	8	55.3	15	41	27	0.175
isotig30913_1644_Z	8	55.3	15	41	27	0.175
isotig30913_630_Z	8	55.3	15	41	27	0.175
isotig30913_822_Z	8	55.3	15	41	27	0.175
isotig38873_388	8	55.3	15	41	27	0.175
isotig38873_618	8	55.3	15	41	27	0.175
isotig31862_140_Z	8	56.5	15	41	27	0.175
isotig30020_476	8	59.0	15	41	27	0.175
isotig22339_503	8	60.9	17	40	25	0.447

^z _Z indicates that the phase of the SNP was unknown and both phases were used for initial mapping, retaining the phase that showed linkage with other phase-known markers. SNPs shown in bold text were mapped for the first time using this segregating family and not previously reported by Duangjit et al. (2013), Damon et al. (2014), or Munaiz and Havey (2020).

^yObs = observed segregations of homozygotes from chartreuse parent (a), homozygotes from B5351 (b), or heterozygotes (h). Codominant segregations at the *G* locus were determined by scoring bulb colors in F₃ families.

Literature Cited

- Damon, S. and M.J. Havey. 2014. Quantitative trait loci controlling amounts and types of epicuticular waxes in onion. *J. Amer. Soc. Hort. Sci.* 139:597–602.
- Damon, S., R. Groves, and M.J. Havey. 2014. Variation for epicuticular waxes on onion foliage and impacts on numbers of onion thrips. *J. Amer. Soc. Hort. Sci.* 139:495–501.
- Duangjit, J., B. Bohanec, A.P. Chan, C.T. Town, and M.J. Havey. 2013. Transcriptome sequencing to produce SNP-based genetic maps of onion. *Theor. Appl. Genet.* 126:2093–2101.
- Duangjit, J., K. Welsh, M. Wise, B. Bohanec, and M.J. Havey. 2014. Genetic analyses of anthocyanin concentrations and intensity of red-bulb color among segregating haploid progenies of onion. *Mol. Breed.* 34:75–85.
- El-Shafie, M. and G. Davis. 1967. Inheritance of bulb color in *Allium cepa*. *Hilgardia* 9:607–622.
- Green, F.N., R. Baur, M. Thomson, and L. McCarthy. 1997. An example of chartreuse skin colour in onion (*Allium cepa* L.) cultivar Greenella. *Genet. Resources Crop Evol.* 44:491–493.
- Goldman, I.L., G. Schroeck, and M.J. Havey. 2001. History of public onion breeding programs and pedigree of public onion germplasm releases in the United States. *Plant Breed. Rev.* 20:67–103.
- Havey, M.J. and C. von Kohn. 2017. Efficacy of molecular markers jnurfl3 and AcPms1 for prediction of genotypes at the nuclear *Ms* locus in North American open-pollinated populations of onion. *HortScience* 52:1052–1053.
- Havey, M.J. and F. Ghavami. 2018. Informativeness of single nucleotide polymorphisms and relationships among onion populations from important world production regions. *J. Amer. Soc. Hort. Sci.* 143:34–44.
- Jones, H.A. and A. Clarke. 1943. Inheritance of male sterility in the onion and the production of hybrid seed. *Proc. Amer. Soc. Hort. Sci.* 43:189–194.
- Jones, H.A. and L.K. Mann. 1963. Onions and their allies. Interscience, New York, NY.
- Khar, A., J. Jakše, and M.J. Havey. 2008. Segregations for onion-bulb colors reveal that red is controlled by at least three loci. *J. Amer. Soc. Hort. Sci.* 133:42–47.
- Kim, S., C.-W. Kim, M. Park, and D. Choi. 2015. Identification of candidate genes associated with fertility restoration of cytoplasmic male sterility in onion (*Allium cepa* L.) using a combination of bulked segregant analysis and RNA-seq. *Theor. Appl. Genet.* 128:2289–2299.
- Kim, S., M.L. Binzel, S. Park, K.S. Yoo, and L.M. Pike. 2004. Inactivation of DFR (Dihydroflavonol 4-reductase) gene transcription results in blockage of anthocyanin production in yellow onions (*Allium cepa*). *Mol. Breed.* 14:253–263.
- King, J.J., J.M. Bradeen, O. Bark, J.A. McCallum, and M.J. Havey. 1998. A low-density genetic map of onion reveals a role for tandem duplication in the evolution of an extremely large diploid genome. *Theor. Appl. Genet.* 96:52–62.
- Leksrisompong, P.P., M.E. Whitson, V.D. Truong, and M.A. Drake. 2012. Sensory attributes and consumer acceptance of sweet potato cultivars with varying flesh colors. *J. Sens. Stud.* 27:59–69.
- Masuzaki, S., M. Shigyo, and N. Yamauchi. 2006. Complete assignment of structural genes involved in flavonoid biosynthesis influencing bulb color to individual chromosomes of shallot (*Allium cepa* L.). *Genes Genet. Syst.* 81:255–263.
- Munaiz, E.D. and M.J. Havey. 2020. Genetic analyses of epicuticular waxes associated with the glossy foliage of ‘White Persian’ onion. *J. Amer. Soc. Hort. Sci.* 145:67–72.
- van Ooijen, J.W. 2006. JoinMap 4, software for the calculation of genetic linkage maps in experimental populations. Kyazma, Wageningen, the Netherlands.
- von Kohn, C., A. Kielkowska, and M.J. Havey. 2013. Sequencing and annotation of the chloroplast DNAs of normal (N) male-fertile and male-sterile (S) cytoplasms of onion and single nucleotide polymorphisms distinguishing these cytoplasms. *Genome* 56:737–742.