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Genetic Analyses of the Shape and Volume of Onion Bulbs and Daylength Effects on Bulbing

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Abstract. The formation of onion (*Allium cepa*) bulbs is affected by photoperiod length and onion germplasm is commonly classified as short- (SD), intermediate-, or long-day (LD) types. The objectives of this study were to develop a segregating family from a cross between doubled haploids (DHs) of LD and SD onions and complete genetic analyses of bulb shape and volume, as well as daylength effects on bulbing. DH parents and F_1 and F_2 progenies were grown in a greenhouse under lengthening days. The diameters of the neck constriction and pseudostems were measured weekly and their ratio was used as the determinant of bulbing. Bulbs were harvested when the foliage collapsed and the diameters and heights of individual bulbs were measured and used to calculate a shape index (diameter divided by height) and bulb volume. Single nucleotide polymorphisms (SNPs) were genotyped and a genetic map of 112 SNPs constructed. Genetic analysis revealed two highly significant quantitative trait loci (QTL) affected bulbing under increasing daylengths, and both QTL showed significant additive effects with no dominance. One highly significant QTL was detected for bulb-shape index and explained 30% of phenotypic variation for bulb shape. Three additional QTL were slightly above the significance threshold, and together these four QTL explained over 50% of the phenotypic variation for bulb shape. No significant QTL were detected for bulb volume. These results reveal that bulb-shape and daylength effects on bulbing are relatively simply inherited, and this research should facilitate introgression of traits between onion populations of different daylength sensitivities and efforts to modify bulb shape.

The formation of onion (*A. cepa*) bulbs is affected by the length of night and temperature (Goldman et al. 2001; Lancaster et al. 1996; Steer 1980); nevertheless, onion germplasm is commonly classified according to length of daylight, as opposed to length of darkness, required for bulb formation (Magruder and Allard 1937). SD and LD onions initiate bulb formation under lengthening periods of light at ~12 and ≥14 h, respectively. Intermediate-day cultivars initiate bulb formation between the daylengths of SD and LD onions. LD cultivars grown under short days may never bulb; SD onions grown under long days initiate bulb formation early and produce bulbs too small to be commercially acceptable. In addition to daylength, bulb formation is affected by temperature. Under the same lighting regimen, higher temperatures hasten bulb formation and plant maturity (Brewster 1994).

Genetic control of daylength response has been extensively studied using model plants such as arabidopsis (*Arabidopsis thaliana)*, and vegetable crops may have similar genetic control (Kim 2020; Taylor et al. 2010). Under the appropriate photoperiod, transcriptional activation of flowering locus T (*FT*) is required for floral induction in arabidopsis (Searle and Coupland 2004). The FT protein is synthesized in the leaves and transported via the phloem to the apical meristem to initiate flowering (Dennis and Peacock 2007). Studies to date on the physiological bases of bulbing in onion have primarily focused on evaluating LD and SD cultivars planted under inductive and noninductive daylengths (Cheng et al. 2021a, 2021b; Lee et al. 2013; Rashid et al. 2019). In onion, six *FT*-like transcripts (*AcFT1* through *AcFT6*) have been identified, two of which are involved in bulbing (Lee et al. 2013). Under noninductive daylengths, *AcFT4* is expressed and acts as a repressor of bulbing. When plants were moved to daylengths inductive for bulbing, expression of *AcFT4* is reduced and expression of *AcFT1* increased to promote bulbing (Cheng et al. 2021a, 2021b; Lee et al. 2013; Rashid et al. 2019).

The sizes and shapes of onion bulbs are important characteristics for consumers and processors. Larger round bulbs are preferred in some markets and by processors for onion rings and diced products; other consumers prefer smaller and/or flatter bulbs. Bulb shape can be evaluated as a shape index (bulb diameter divided by height or the inverse ratio) (Clark and Heath 1962; Magruder et al. 1941) and there have been numerous studies estimating heritability of bulb shape. Salem (1966) reported broad-sense heritabilities of 44% to 59% for bulb-shape indices among flat, high globe, and torpedo-shaped cultivars. Narrow-sense heritabilities for bulb-shape indices across diverse onion populations were relatively high at 17% to 68% (Dowker and Fennell 1974; McCollum 1966, 1971; Naxamoba 1958). The height of bulbs showed higher narrow-sense heritability (25% to 76%) than shape index or bulb diameter (McCollum 1966, 1971). These relatively high heritability estimates are consistent with selection responses; McCollum (1966) wrote that the torpedo-shaped cultivar 'Italian Red' was selected in a few generations from the relatively flat cultivar 'California Early Red'. In contrast, the sizes and weights of bulbs had narrow-sense heritabilities from 0% to 11% (McCollum 1966, 1971; Naxamoba 1958).

The hypotheses tested by this research were that the shape and volume of onion bulbs, as well as daylength effects on

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bulbing, are genetically determined allowing for selection and modification of these important bulb characteristics.

Materials and Methods

DH parents and development of segregating family. DH1104 and DHCU66619 were obtained from Bayer AG (Leverkusen, Germany) and Cornell University (Ithaca, NY, USA), respectively. DH1104 originated from the cross of 'Texas Early Grano 1015Y' (1015Y) with 'Ben Shemen' (Dr. Rick Jones, Bayer, personal communication). '1015Y' and 'Ben Shemen' are onion cultivars historically grown in the southern United States at latitudes of ~26° to 33° north, respectively. '1015Y' is an SD onion sown in the fall in southern Texas; plants remain in the field over the winter, and bulbs are produced early in the spring under relatively short days and harvested in May to June. 'Ben Shemen' is an ID cultivar commonly spring-planted in the southern United States and was derived from a Californian (USA) selection of 'Sweet Spanish' onion (Cramer and Corgan 2003). DHCU66619 was extracted from a synthetic population produced by intercrossing among LD onions grown in the state of New York, USA (Hyde et al. 2012). This LD germplasm is spring seeded and bulbs form under long days at ~42° north and fall harvested. The genetic homozygosity of both DHs was established by genotyping 247 SNPs evenly distributed across the eight chromosomes of onion (Havey and Ghavami 2018) as described in the following. The cytoplasms [normal (N) male-fertile vs. male-sterile (S)] of the DHs were established using the accD polymorphism described by Von Kohn et al. (2013).

Plants of DHCU66619 were grown in a field on the Kincaid family farm (Palmyra, WI, USA) under normal production conditions for LD onion. Bulbs were harvested in the fall and vernalized at 4 °C for 7 months. Seed of DH1104 was planted in early September in a greenhouse on the University of Wisconsin (UW) campus in pots of 11.4 cm diameter and containing a soilless mix (PRO-MIX HP Mycorrhizae; Premier Tech Horticulture, Quakertown, PA, USA) with supplemental lighting at 11 h and a constant temperature of 25 °C. In early January, plants of DH1104 were moved to a cold room with a constant temperature of 6 °C and supplemental lighting at 11 h. Vernalized plants (DH1104) and bulbs (DHCU66619) were planted together in early May in a field at the UW Experimental Farm at Arlington, WI, USA. Umbels on flowering plants were covered with mesh cages (Havey 2018) and pupae of blue-bottle flies (*Diptera calliphoridae*) were obtained (Forked Tree Ranch, Bonners Ferry, ID, USA) and placed into the cages for crossing. In August, seed was harvested separately from each DH parent, cleaned, and planted in a greenhouse on the UW campus in early September. DNA was isolated from individual progenies and hybrids between DH1104 and DHCU66619 were identified by SNP heterozygosity as described in the following. Hybrids were allowed to grow in the greenhouse until early January with supplemental lighting of 11 h and temperatures between 23 and 28 °C. Hybrid plants were then moved to a cold chamber as described previously until early May, when they were transplanted to a field near Arlington, WI, USA. Hybrids were caged and fly pupae introduced as described previously to produce the segregating F_2 family.

Phenotypic measurements of bulbing. Seeds of the parental DHs, their hybrid, and F_2 progenies were planted on 1 Oct in a greenhouse on the UW campus in seedling trays with 6 cm × 6 cm cells containing the soilless mix (described previously) with supplemental lighting at 11 h and a daytime temperature of 25 °C with 20 °C nights. Forty-six days after seed sowing, plants had three to four true leaves and were transplanted into 15.5-cm plastic pots containing the soilless mix and grown in a greenhouse with temperatures of 25 °C days and 20 °C nights and 11 h of supplemental lighting provided by 400-W high pressure lamps with 75-W grow lights (Shengsite, Monrovia, CA, USA) added to augment light in the red (660 to 670 nm) and blue (460 to 470 nm) spectrum at 3:1 red:blue lamp bead quantities (Mondal et al. 1986). At least six plants of each of the parental DHs and their hybrid and 179 F_2 progenies were randomly placed on greenhouse benches. Photosynthetic photon flux density provided by the supplemental lighting was 71 ± 9 $\mu mol \cdot s^{-1} \cdot m^{-2}$ at the top of the pots. The walls of the greenhouse were covered with black tarps to exclude light from adjacent greenhouses or outdoors; the top of the greenhouse was not covered. Plants were fertilized twice weekly with 20N–8.7P–16.6K (Peters Professional 20–10–20; Everris, Dublin, OH, USA) with micronutrients (Peat-Lite Special, Allentown, PA, USA) providing 300 ppm nitrogen. On 10 Jan, most of the plants had six to eight leaves and the length of supplemental lighting was increased by 15 min every week. Once per week starting in early January through the end of May (11 to 15 h of daylength, respectively), bulbing was measured as described by Clark and Heath (1962). A digital caliper was used to measure the neck diameter, and then the plant was rotated 90° on its axis and a second reading of neck diameter was taken. Two measurements of the pseudostem were taken at the position of maximum diameter between the neck and basal plate. The neck and pseudostem measurements were averaged, the mean pseudostem diameter was divided by the mean neck diameter, and a ratio of 2.0 was considered as the indicator of bulbing (Clark and Heath 1962). Measurements were taken on each F_2 progeny and plants of the parental DHs and their hybrid until the bulb-to-neck ratio of a plant was ≥2.0. It is important to note that because daylength was recorded when the bulb-to-neck ratio reached 2.0, the actual daylength at which bulbing was initiated was shorter and it was assumed that the time from initiation of bulbing until the bulb-to-neck ratio reached 2.0 was similar across the parents, hybrid, and F_2 progenies. Bulbs were harvested after foliage had collapsed ("tops down") and allowed to dry in a greenhouse for ~10 d. The maximum diameter of each bulb was measured and then the bulb was rotated 90° on its axis and a second reading of diameter was taken. Two measurements of bulb height were taken from the basal plate to the base of the neck constriction. The two measurements of diameter and height were averaged and a bulb-shape index was calculated by mean diameter divided by mean height. Bulb volume in mm^3 was calculated as the volume of an ellipse ($4/3 \times \pi \times A \times B \times C$, where A and B are the bulb radii calculated as one-half of the two bulb-diameter measurements and C is one-half of the mean bulb-height measurement).

DNA extraction and genotyping of SNPs. Leaf tissues were collected from the parental DHs, individual F_1 plants, and F_2 progenies and DNAs were extracted using a minipreparation (NucleoSpin Plant II Midi DNA Purification kit, Macherey-Nagel, Duren, Germany). DNA quantity was measured spectrophotometrically (NanoDrop; Thermo-Fisher Scientific, Waltham, MA, USA) and quality was assessed by electrophoresis of the DNA through 1%-agarose gels followed by visual examination for clear bands

migrating with uncut λ DNA. DNAs from the DH parents were genotyped for 247 SNPs evenly spread across the eight chromosomes of onion using the KASPar platform (Duangjit et al. 2013; Havey and Ghavami 2018), of which 112 were polymorphic. Genetic mapping was completed using JoinMap 5.0 (Van Ooijen 2018), and linkage groups constructed and marker order resolved using logarithm of odds (LOD) of linkage = 7.0. Linkage groups were assigned to chromosomes using previously mapped SNPs (Damon and Havey 2014; Duangjit et al. 2013).

Statistical and genomic analyses. For mapping of daylength effects on bulbing, bulb shape, and bulb volume, SNP genotypes of segregating progenies and respective phenotypes were analyzed by imputation (sim.geno), scanone, scantwo, and forward/backward selection (stepwiseqtl) with the R/qtl and R/Broman packages (Broman and Sen 2009; Broman et al. 2003) in RStudio 2022.07.2 + 576 "Spotted Wakerobin" release (R Foundation for Statistical Computing, Vienna, Austria). For all analyses, 1000 permutations were completed to determine the 0.05 significance LOD threshold. After identifying a QTL, the maximum LOD score, additive and dominance effects, 1.5-LOD interval, and percent phenotypic variation explained by the QTL were calculated. The genomic locations of FT homologs and major QTL affecting bulbing were identified with blastn searches (Priyam et al. 2019) to the onion genome (Finkers et al. 2021) using the messenger RNA (mRNA) sequences of AcFT1 and AcFT4 (Genbank accessions KC485348.1 and KC485351.1, respectively) and sequences flanking the most significant SNPs.

Results and Discussion

Molecular marker genotyping of DH parents and segregating family. Complete homozygosity of DH1104 and DHCU66619 was confirmed by genotyping 247 SNPs distributed across the eight chromosomes of onion (Havey and Ghavami 2018). Both DHs possess normal male-fertile cytoplasm as determined by the accD polymorphism (Von Kohn et al. 2013). A total of 112 SNPs were polymorphic between DH1104 and DHCU66619, of which 104 fit the expected F_2 segregation ratio of 1:2:1 at $P > 0.01$ (Supplemental Table 1). Significant deviations

Table 1. Mean hours of daylength at which the bulb-to-neck ratio was ≥ 2.0, mean bulb shape index (ratio of diameter·over height), and mean square root (sqrt) of bulb volumes (in millimeters^3) with standard deviations (*SD*s) for onion doubled haploid (DH) 1104 and DHCU66619 and the F_1 and F_2 families from the cross of DH1104 by DHCU66619.

	Daylength in hours when bulb-to-neck ratio ≥2.0		Bulb			
			Shape index		Sqrt (volume)	
Parent or family	Mean[i]	*SD*	Mean[i]	*SD*	Mean[i]	*SD*
DHCU66619	16.2	0.3 a	1.14	0.14 a	218.2	60.2 b
DH1104	14.7	0.1 b	1.01	0.63 a	273.7	95.6 ab
F_1	14.5	0.3 b	1.15	0.08 a	402.3	93.4 a
F_2	15.2	0.6 b	1.09	0.14 a	315.3	96.7 a

[i] Means followed by the same letter were not significantly different using Fisher-least significant difference test with the Bonferroni correction at $P = 0.05$.

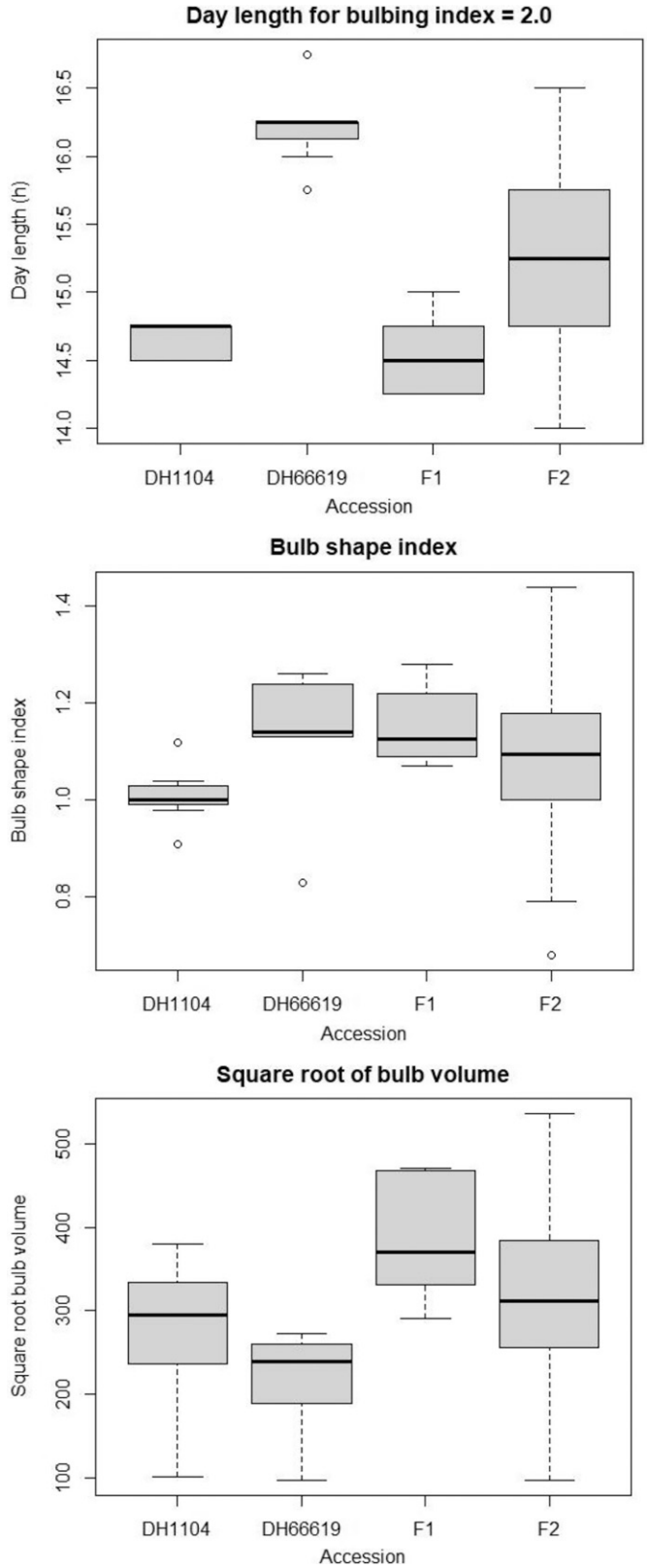

Fig. 1. Box plots of daylength in hours (h) at which onion plants reached a bulb-to-neck ratio of at least 2.0, bulb-shape index (ratio of diameter over height), and the square root of bulb volume (millimeters^3) for short-day doubled haploid (DH) 1104; long-day DHCU66619; and the F_1 and F_2 progenies from the cross of DH1104 by DHCU66619.

($P \leq 0.001$) from expected segregation ratios were observed for six SNPs on chromosome 1 and two SNPs on chromosome 4; segregations across the other genomic regions fit expected ratios (Supplemental Table 1).

Genetic analysis of bulbing under increasing daylengths. The Shapiro-Wilk normality test revealed that the daylengths at which the bulb-to-neck ratios reached 2.0 were normally distributed ($P = 0.10$). There were significantly ($P < 0.001$) different daylengths at which the bulb-to-neck ratios reached 2.0 for LD DHCU66619 vs. SD DH1104 (Table 1). Mean daylength of bulbing for hybrid plants from DH1104 × DHCU66619 and the F_2 family were not significantly different from their SD parent (Table 1). The F_2 family from DH1104 × DHCU66619 showed evidence of transgressive segregation for bulbing relative to the mean daylengths of the DH parents (Fig. 1).

Quantitative analysis of daylengths at which bulb-to-neck ratios reached 2.0 in the F_2 family revealed two highly significant QTL, one each on chromosomes 5 and 6 (Table 2). The most significant SNP (isotig26178_547) on chromosome 5 showed a highly significant additive effect (Table 2; Fig. 2) that increased daylength for bulbing by 0.26 h (15.6 min) for each copy of the chromosome region from LD DHCU66619 (Table 2). On chromosome 6, the most significant SNP (isotig40098_630) also showed highly a significant additive effect (Fig. 2) of the region from DHCU66619 to increase daylength for bulbing by 0.33 h (19.8 min) for each copy of the chromosome region from LD DHCU66619 (Table 2). There was no significant dominance at both QTL (Table 2) and no significant ($P > 0.05$) interaction between the QTL, indicating that the two QTL act independently to affect the daylength required for bulbing. The highly significant ($P < 0.001$) additive effects and lack of dominance of both QTL on daylengths for bulbing indicate that crosses between SD and LD onions will produce hybrids that bulb intermediate to the parents, and a breeder could select for chromosome regions from the SD parent to quickly recover the SD phenotype, from the LD parent to recover the LD phenotype, and contrasting QTL on chromosomes 5 and 6 to select for daylength response intermediate relative to the two parental phenotypes. These results should be useful for the introgression of traits between onions with different daylength requirements for bulbing and subsequently recover the desired daylength response.

AcFT4 and *AcFT1* are associated with repression and induction of bulbing, respectively; when bulbing is initiated, expression of AcFT4 is reduced and AcFT1 is enhanced (Cheng et al. 2021a, 2021b; Lee et al. 2013; Rashid et al. 2019). BLAST searches of the mRNA sequences of AcFT1 and AcFT4 to the onion genome database (Finkers et al. 2021) confidently (100% identities) placed these two genes on Scaffold_75766 and Scaffold_73326, respectively. The genomic sequences flanking SNPs across the LOD-1.5 intervals on chromosomes 5 and 6 (Table 2) did not show any similarities to sequences on these two scaffolds; however, the relatively small family size and number of genetic markers limit positioning of the major QTL affecting bulbing. The additive nature of the two major QTL affecting bulbing differs from the expected dominance of a repressor (AcFT4) or inducer (AcFT1) of

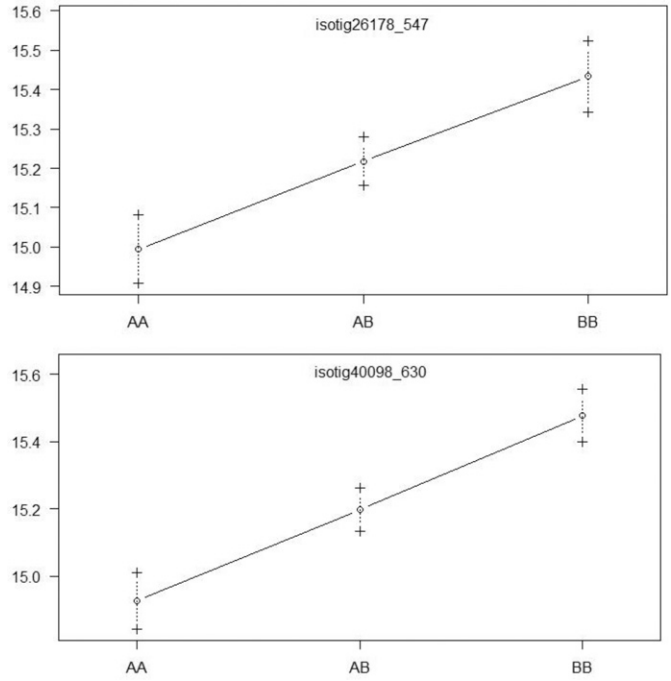

Fig. 2. Plots showing additive effects of chromosome regions from long-day doubled haploid (DH) onion CU66619 that increase the daylength for bulbing relative to chromosome region from short-day DH1104. Single nucleotide polymorphism (SNP) isotig26178_547 is on chromosome 5 (top graph) and SNP isotig40098_630 is on chromosome 6 (bottom graph). On the x-axis, A indicates chromosome region from short-day DH1104 and B the region from long-day DHCU66619. The y-axis shows hours of daylight at which the bulb-to-neck ratio was at least 2.0.

Table 2. Onion chromosome (Chr) and position in centimorgans (cM) of the most significant single nucleotide polymorphism (SNP), SNPs flanking the 1.5 logarithm of odds (LOD) confidence interval, percent variation (%Var) explained, observed LOD with threshold (Thresh) values from permutation analysis, and additive (Add) and dominance (Dom) effects of chromosome regions from long-day doubled haploid (DH) CU66619 for quantitative trait loci affecting bulb-shape index (ratio of diameter·over height), and daylengths in hours at which the bulb-to-neck ratio was ≥2.0 in F_2 family from the cross of short-day doubled haploid (DH)1104 by long-day DHCU66619.

							Effect			
Trait	Chr@cM	SNP[i]	1.5-LOD interval	%Var	LOD	Thresh	Add[ii]		Dom[ii]	
Bulbing	5@11	isotig26178_547	isotig31940_1090 to isotig34069_110	9.4	4.17	3.43	0.260	***	−0.004	NS
“	6@38	isotig40098_630	isotig29476_1380 to isotig33185_668	15.1	6.64	3.43	0.330	***	−0.043	NS
Bulb shape index	1@24	isotig37265_852	isotig29661_1491 to isotig36532_752	5.2	3.3	3.21	−0.047	*	0.017	NS
“	1@65	isotig27537_659	isotig29923_361 to isotig32065_872	29.8	15.9	3.21	0.113	***	−0.014	NS
“	5@17	isotig37670_180	isotig31940_1090 to isotig33965_554	8.3	5.2	3.21	−0.056	**	0.016	NS
“	7@28	isotig34668_1112	isotig26063_406 to isotig34668_1112	7.3	4.6	3.21	0.051	**	−0.011	NS

[i] SNPs were described by Duangjit et al. (2013).
[ii] Significance of $P < 0.05$ (*), < 0.01 (**), and < 0.001 (***); NS = not significant ($P > 0.05$).

Fig. 3. Examples of contrasting onion bulb-shape indices (ratio of diameter over height) of two F_2 progenies from the cross of doubled haploid (DH) 1104 and DHCU66619.

bulbing. For example, production of an inducer would be expected to show dominance over no inducer. In the case of AcFT4, removal of the repressor, for example by RNA interference, would also be expected to show dominance. Therefore, the two major QTL associated with bulbing under increasing daylengths are likely involved with regulation of AcFT1 and AcFT4.

Genetic analyses of bulb shape and volume. After foliage collapsed at the neck, bulb diameters and heights were measured for the parental DHs, hybrid progenies, and the F_2 family. A shape index (ratio of diameter over height) (Fig. 3) and volume (ellipsoid volume in mm^3) were calculated for each bulb. Shapiro-Wilk tests revealed that shape indices were normally distributed ($P = 0.099$). The mean bulb-shape indices for DH1104, DHCU66619, and their hybrid progenies were not significantly ($P > 0.05$) different (Table 1). However transgressive segregation was observed among the F_2 progenies and quantitative analysis of the bulb-shape indices revealed one major QTL on chromosome 1 at 65 cM explaining 30% of the phenotypic variation for bulb shape (Table 2). The chromosome region from DHCU66619 showed significant additive effects (Table 2; Fig. 4) to increase the bulb-shape index, meaning that it conditioned flatter bulbs. There were three additional QTL significantly affecting bulb-shape index, another one on chromosome 1 at 24 cM and one each on chromosomes 5 at 17 cM and 7 at 28 cM; however, the significances of each of these regions were just above the LOD thresholds and together the three QTL explained 21% of the phenotypic variation (Table 2). All four QTL accounted for 51% of the phenotypic variance for bulb shape. This result agrees with previous studies documenting relatively large narrow-sense heritabilities for bulb shape across diverse onion populations (McCollum 1966, 1971; Naxamoba 1958).

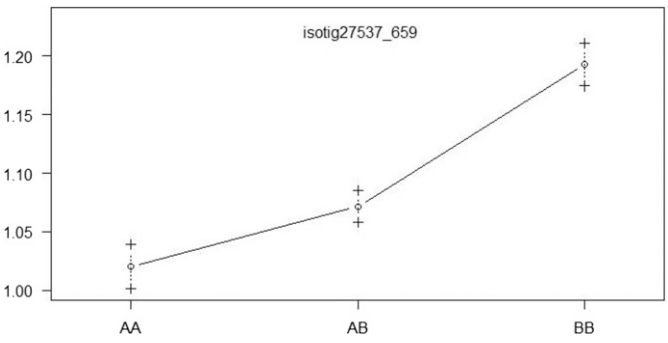

Fig. 4. Plot showing effects of onion chromosome region from long-day doubled haploid (DH) CU66619 that increases bulb-shape index (ratio of diameter over height) relative to chromosome region from short-day DH1104. Isotig27537_659 is a single nucleotide polymorphism on chromosome 1 that had the greatest significant effect on the bulb-shape index. On the x-axis, A indicates chromosome region from short-day DH1104 and B the region from long-day DHCU66619. The y-axis shows bulb-shape indices.

Bulb volumes significantly deviated from normality (Shapiro-Wilk test $P = 4.2 \times 10^{-6}$), and the square root transformation of bulb volumes was used to normalize observations ($P = 0.153$). The mean square root transformations of bulb volumes for DH1104 (273.7 mm^3) and DHCU66619 (218.2 mm^3) were not significantly ($P > 0.05$) different (Table 1). Hybrid progenies from the cross of DH1104 by DHCU66619 had larger mean volumes (383.7 mm^3) as expected due to hybrid vigor (Jones and Davis 1944), but were only significantly ($P > 0.05$) greater than the DHCU66619 parent (Table 1). Quantitative analysis of bulb volumes in the F_2 family revealed no significant QTL, in agreement with previous studies reporting heritabilities at or near zero for bulb size (McCollum 1966, 1971; Naxamoba 1958).

Conclusions

This is the first study of daylength effects on bulbing using a segregating family from the cross of SD by LD onions. Bulbing was controlled by two significant QTL, one each on chromosomes 5 and 6 (Table 2). There was no significant interaction between these two QTL and chromosome regions from the LD parent additively increased the daylength required for bulbing. These results should be useful for trait introgression between onion populations of different daylength requirements. Fine mapping and expression analyses will be required before candidate genes can be identified for the major QTL associated with bulbing, and their interaction with FT homologs determined. Eventual modification of genes associated with induction of bulbing may help to develop daylength-insensitive onion.

Bulb shape in this family was affected by four QTL, one of which on chromosome 1 explained the greatest amount (~30%) of the phenotypic variation for this trait. These results are in agreement with previous studies (McCollum 1966, 1971; Naxamoba 1958) and indicate that phenotypic selection should be effective to alter bulb shape. No QTL were detected for bulb size, which has been previously reported to show low heritability (McCollum 1966, 1971; Naxamoba 1958). Overall bulb size may be largely determined by length of growing season, temperature and light levels, bulb maturity, and planting density, among other environmental factors.

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