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Mapping of the Egusi Seed Trait Locus (*eg*) and Quantitative Trait Loci Associated with Seed Oil Percentage in Watermelon

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Abstract. **The egusi watermelon (*Citrullus lanatus*) is popular in West Africa for its oil and protein-rich seed, which is consumed in soups and stews. The egusi phenotypic trait is controlled by a single recessive gene (*eg*) and is characterized by large seed size and fleshy, thick pericarp. An F_2 mapping population was derived from Strain II (PI 279461) of the Japanese cultivar Yamato-cream with normal seed type and low seed oil percentage (SOP = 25.2%) and an egusi type from Nigeria [Egusi (PI 560023)] with high SOP (40.6%). Genetic analysis confirmed that the egusi seed trait is controlled by a single recessive gene (*eg*) and the location of the gene was mapped to 57.8 cM on linkage group (LG) 2, between markers NW0248325 and NW0250248. Four main quantitative trait loci (M-QTL) were identified for SOP in the population with the *eg* locus contributing 84% of the explained phenotypic variation (R^2). A significant epistatic interaction (E-QTL) was identified between, the *eg* locus and an M-QTL on LG 9B. The present study reports the location of the *eg* locus responsible for the egusi seed trait in watermelon on LG 2 as well as M-QTL and E-QTL associated with SOP.**

Egusi seed is a part of the daily diet in many West African countries, including Ghana, Nigeria, and Benin [National Research Council of the National Academies (NRC), 2006]. Although the term "egusi" can be used to describe a certain seed type from several species of the Cucurbitaceae family (Achigan-Dako et al., 2008; NRC, 2006), it is often used in reference to egusi watermelon. The plants cultivated for their oil and protein-rich seeds are currently classified as *C. lanatus* ssp. *mucosospermus* var. *egusi* (Fursa, 1972; Jeffrey, 2001) and have sometimes been misclassified as *C. colocynthis* (Gusmini et al., 2004; Jarret et al., 1997; Robinson and Decker-Walters, 1997; Wehner, 2008). However, chloroplast (Dane and Lang, 2004; Dane and Liu, 2007) and nuclear (Che et al., 2003; Jarret et al., 1997; Nimmakayala et al., 2010) genetic studies do not support the subspecies classification and groups egusi types with cultivated watermelon (*Citrullus lanatus* var. *lanatus*).

The egusi watermelons are unique because they contain large, flat seeds that are enclosed in a fleshy pericarp. The flesh of the fruit is dry and bitter but the ground-up seed serves as a rich source of protein, carbohydrates, and vitamins in soups, stews, and seasonings (Achigan-Dako et al., 2008; NRC, 2006; Ntui et al., 2010). Egusi seeds can contain up to 50% oil (Achu et al., 2005) and 28% protein (Achu et al., 2005; Bankole et al., 2005). The oil produced from the seeds can serve as a valuable source of energy in the regions where it is grown and it has been reported that the composition of egusi oil is comparable to safflower (*Carthamus tinctorius*), soybean (*Glycine max*), and sunflower (*Helianthus annuus*) oil as a feedstock for biodiesel production (Giwa et al., 2010; Jarret and Levy, 2012).

The egusi seed trait is controlled by a single recessive gene (Gusmini et al., 2004), but the nature of the gene and its origin is unknown. Various approaches can be followed to determine the nature of a gene, including positional cloning, which requires knowledge of the location of a gene in the genome. Until recently the genetic resources needed for such an undertaking were not available in watermelon. However, recently a single nucleotide polymorphism (SNP) map was developed for an F_2 population segregating for the egusi seed phenotype as well as SOP (Prothro, 2010; Sandlin et al., 2012). We used this resource to 1) determine the genomic location of the *eg* locus in watermelon; and 2) identify M-QTL and E-QTL associated with SOP in a population segregating for the egusi seed trait.

Materials and Methods

Seed of watermelon accessions and cultivars with normal or egusi seed types were obtained from the U.S. Department of Agriculture–Agricultural Research Service germplasm collection (Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, Griffin, GA) (Table 1). Seed of the cultivar Crimson Sweet and the selection Egun were obtained from Johnny's Selected Seed (Winslow, ME) and G.E. Boyhan (University of Georgia, Athens, GA), respectively. Near magnetic resonance [NMR (MiniSpec MQ20 NMR analyzer; Bruker Optics, Billerica, MA)] was used to determine

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Table 1. Seed type and seed oil as a percentage of seed weight (SOP) of watermelon cultivars and PIs as determined by near magnetic resonance (NMR).[z]

Accession/cultivar[y]	Seed type	SOP (%)
PI 635617 ('New Hampshire Midget')	Normal	20.14
PI 635609 ('Klondike Black Seeded')	Normal	22.29
PI 279461 (Strain II)	Normal	25.20
PI 244019[x]	Normal	25.37
'Crimson Sweet'	Normal	26.55
PI 593359	Normal	27.05
PI559999	Egusi	30.30
PI559993	Egusi	30.85
PI559992	Egusi	30.91
PI560018	Egusi	31.82
PI560008	Egusi	33.00
PI560017	Egusi	33.08
PI560004	Egusi	33.18
PI560000	Egusi	33.24
PI560014	Egusi	33.69
PI560019	Egusi	34.20
PI560003	Egusi	34.39
PI559997	Egusi	34.77
PI560002	Egusi	34.98
PI559994	Egusi	35.78
PI559996	Egusi	36.03
PI560005	Egusi	36.29
PI560010	Egusi	36.60
PI560020	Egusi	36.66
PI560007	Egusi	36.73
PI560012	Egusi	36.88
PI560001	Egusi	37.01
PI560015	Egusi	37.06
PI559995	Egusi	37.12
PI560009	Egusi	37.21
PI560006	Egusi	37.37
PI560016	Egusi	38.19
PI560013	Egusi	39.02
PI560011	Egusi	39.22
Egun[w]	Egusi	40.08
PI560024	Egusi	40.47
PI 560023	Egusi	40.60

[z]Samples are ordered from lowest to highest SOP. The parents used for the mapping population are underlined.

[y]'Crimson Sweet' was obtained from Johnny's Selected Seed (Winslow, ME), whereas Egun was supplied by G.E. Boyhan (University of Georgia, Athens, GA). All other cultivars and accessions were obtained from the U.S. Department of Agriculture–Agricultural Research Service, National Plant Germplasm System, Plant Genetic Resources Conservation Unit, Southern Regional Plant Introduction Station, Griffin, GA.

[x]*Citrullus lanatus* var. *citroides*.

[w]Selection from PI 595203 (Ling et al., 2009; Murphy and Dane, 2009).

SOP as described by Burke et al. (2005) and Wills et al. (2010) for sunflower seeds but using watermelon seed standards. Briefly, at least 20 seeds (1.83 to 5.43 g) of each cultivar/accession were transferred to a flat-bottomed sample tube and total seed oil was determined as a percentage of seed weight.

An F_2 mapping population of 187 individuals was developed using 'Yamato-cream' Strain II (Strain II; PI 279461) from Japan and a wild Nigerian egusi type [Egusi (PI 560023)] (Fig. 1). The development of the Strain II × Egusi F_2 genetic map is described elsewhere (Prothro, 2010; Sandlin et al., 2012). Briefly, the map includes 357 SNP markers on 14 LGs with an average distance of 4.2 cM between markers.

Fig. 1. Seed from the parents [Strain II (PI 279461) and Egusi (PI 560023)] used to develop the watermelon mapping population. The bar represents 1 cm.

The F_2 population and parents were direct-seeded in the field at the University of Georgia's Plant Science Farm in Watkinsville in Summer 2007. Plants were grown according to University of Georgia Cooperative Extension Service recommendations. One mature fruit from 142 individuals was harvested and seeds from each fruit were cleaned and collected by hand. Seed was scored as egusi or normal based on visual inspection and allowed to dry before determining SOP as described previously. Because SOP is a proportion of weight, the data were arcsine square root transformed before QTL analysis (Sokal and Rohlf, 1995; Wills et al., 2010).

After confirming mendelian inheritance fitting a 3:1 ratio, the normal trait was coded as a dominant marker (d,b) and mapped onto the existing Strain II × Egusi SNP map using JoinMap 4.0 (Kyazma, Wageningen, The Netherlands).

Analysis for the detection of M-QTL was performed using composite interval mapping [CIM (Zeng, 1993, 1994)] and multiple interval mapping [MIM (Kao and Zeng, 1997; Kao et al., 1999; Zeng et al., 1999)] in WinQTL Cartographer (WinQTL Cart) Version 2.5 (Wang et al., 2011). Because the F_2 plants in the field were open-pollinated, the population type was designated as "RF3" (Wang et al., 2010). For CIM, permutation tests (1000 permutations, $\alpha = 0.05$) were used to determine the threshold values for each trait (Churchill and Doerge, 1994; Doerge and Churchill, 1996). CIM analysis was performed using the standard model (Model 6) with a walk speed of 1 cM and forward–backward stepwise regression to set the number of marker cofactors. The cofactors within 10 cM on either side of the QTL were excluded from the model. E-QTL was detected using MIM, and significance was determined as recommended by the authors using the information criteria $IC(k) = -2[\log(L) - kc(n)/2]$ and penalty function $c(n) = \log(n)$. All LGs and QTL were visualized using MapChart 2.2 (Voorrips, 2002).

Results and Discussion

Total SOP of accessions with egusi seed type ranged from 30.30% to 40.60%, whereas values for the samples with normal seed ranged from 20.14% to 26.55% (Table 1). These results are

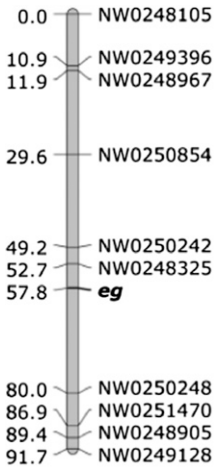

Fig. 2. Genetic map of watermelon linkage group 2 in the Strain II (PI 279461) × Egusi (PI 560023) F_2 population showing the location of the *eg* locus controlling the egusi seed phenotype.

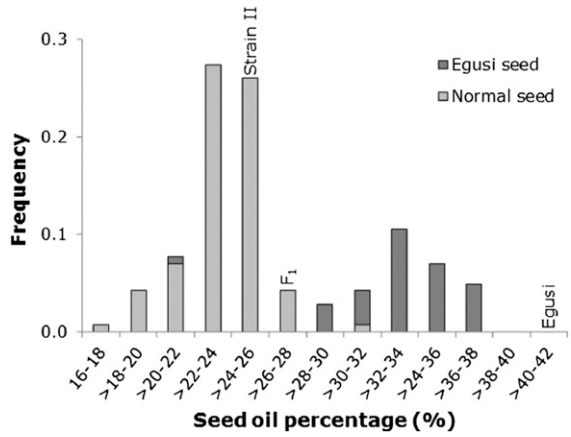

Fig. 3. Frequency distribution of watermelon seed oil as a percentage of seed weight in the Strain II (PI 279461) × Egusi (PI 560023) F_2 population. The distribution of normal and egusi seed within the population as well as the phenotypes of the parental and F_1 seed are indicated.

Table 2. Main effect quantitative trait loci (M-QTL) and epistatic effect QTL (E-QTL) identified for seed oil as a percentage of seed weight (SOP) in the Strain II (PI 279461) ± Egusi (PI 560023) F_2 watermelon population using multiple interval mapping (MIM) (Kao and Zeng, 1997; Kao et al., 1999; Zeng et al., 1999).

M-QTL							
LG[z]	Position (cM)	LOD[y]	R^2 (%)[x]	Additive effect[w]	Dominance effect[w]	LOD-1 support interval (cM)	LOD-1 support interval (cM)
2	42.6	1.90	–5.95	0.0091	0.0096	31.1	51.0
2	57.7	18.94	83.88	–0.0478	–0.0724	54.9	61.9
2	81.0	4.50	9.26	–0.0147	–0.0025	78.7	84.6
9B	86.2	3.48	1.31	0.0059	0.0144	77.3	95.1
E-QTL							
LG	Type of interaction[v]	LOD	R^2 (%)	Phenotypic effect[w]			
2 (57.7) × 9B	D × A	2.31	0.7	–0.0198			

[z]Linkage group.
[y]Log_{10} likelihood ratio.
[x]Phenotypic variation explained (R^2).
[w]Negative values indicate that the effect is contributed by the allele from PI 560023 (Egusi). The results are for the arcsine square root transformed data.
[v]Dominant × additive.

similar to a results obtained in a recent study by Jarret and Levy (2012). Earlier research has reported seed oil content as high as 50% to 53% (Bankole et al., 2005; El-Adawy and Taha, 2001) in *C. lanatus*. However, the latter studies involved oil extracted from the kernel only, which is expected to have higher oil percentage than whole seed with a positive correlation ($r = 0.82$) reported between the two traits in sunflower (Leon et al., 1995).

In the Strain II × Egusi F_2 population, 42 fruit had the egusi seed phenotype, whereas 100 had the normal seed phenotype. A chi-square goodness-to-fit test showed that the trait fit a 3:1 ratio ($\chi^2 = 1.59$, df = 1, $P > 0.05$), confirming the results of Gusmini et al. (2004) that the egusi seed phenotype is controlled by a single recessive gene. The *eg* locus mapped between marker NW0248325 and NW0250248 to position 57.8 cM on LG 2 of the Strain II × Egusi genetic map (Fig. 2). NW0248325 is the closest marker to the *eg* locus, but the marker is still 5.1 cM from the *eg* locus.

The SOP in the F_2 population ranged from 17.8% to 37.8% (Fig. 3). With the exception of two samples, all normal seed had SOP below 28%, whereas all egusi seed had SOP above 28%.

CIM and MIM yielded similar results and both identified four M-QTL for SOP in the F_2 population (MIM results in Table 2). Three QTLs were identified on LG 2 and one on LG 9B. The QTL identified at the 57.7 cM position on LG 2 overlaps with the mapped position of the *eg* locus (Fig. 4) and is responsible for ≈84% of the R^2. This result is in line with the distribution of the SOP phenotype in the population (Fig. 3), which shows a clear delineation between samples with the egusi seed phenotype and normal seed phenotype.

Two other M-QTLs were identified on LG 2, one at 42.6 cM and another at 81.0 cM (Table 2; Fig. 4). Unfortunately, there are few markers in the area surrounding the *eg* locus on LG 2 and the distance between markers is large. This makes it difficult to determine whether these two M-QTLs truly represent additional M-QTL on LG 2 or whether they are artifacts of the major effect *eg* locus. In an effort to elucidate this matter, the F_2 population was divided based on seed type (normal or egusi) and mapped as two separate populations. This approach eliminated the effect of the *eg* locus, but also drastically lowered the size for mapping populations. In the normal seed population (n = 100), an M-QTL

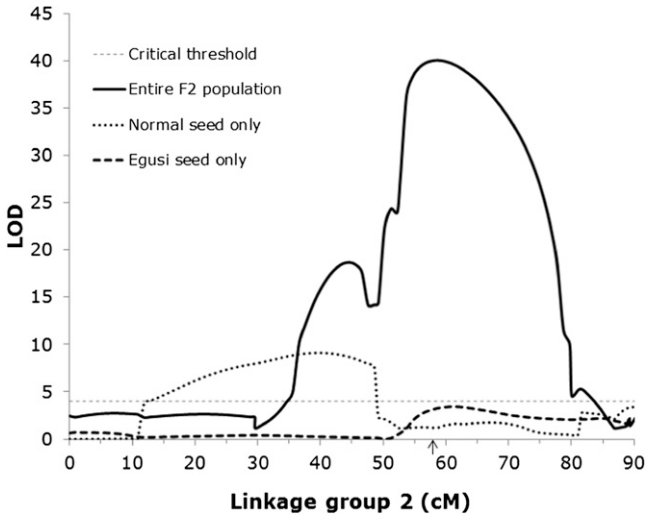

Fig. 4. Log_{10} likelihood ratio (LOD) curves of main effect quantitative trait loci on linkage Group 2 associated with seed oil as a percentage of seed weight in the watermelon Strain II (PI 279461) × Egusi (PI 560023) F_2 population. Results shown are from composite interval mapping (Zeng, 1993, 1994) analysis of the entire F_2 population as well as analysis of normal seed and egusi seed separately. The arrow on the x-axis indicates the posigion of the egusi (*eg*) locus.

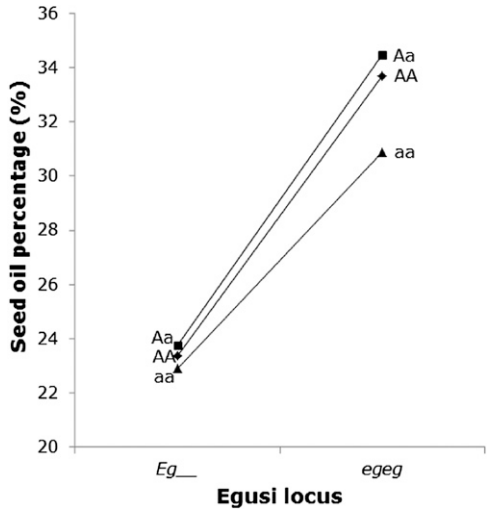

Fig. 5. Epistasis plot (Kao and Zeng, 2002; Kao et al., 1999) for the interaction between the egusi locus (*eg*) on linkage group (LG) 2 and the main effect quantitative trait loci (M-QTL) on LG 9B in the watermelon Strain II (PI 279461) × Egusi (PI 560023) F_2 population. A and a represent the alleles of the marker (NW0249185) closest to the quantitative trait loci on LG 9B.

was identified at position 39.61 cM [1-LOD (log_{10} likelihood ratio) support interval: 30.7 to 46.9 cM] confirming the presence of an additional M-QTL (other than *eg*) on LG 2 (Fig. 4). A QTL associated with seed size has been mapped in this region of LG 2 in watermelon (Prothro, 2010), suggesting that seed size plays a role in SOP, at least in normal seeds. At 81 cM, the LOD curve does not cross the critical threshold, so the M-QTL at this position still remains debatable. No QTLs were identified when only egusi seed were used for mapping, probably as a result of the small population size (n = 42). Current efforts are underway to map additional markers in the region of the *eg* locus on LG 2 to further shed light on the region.

In addition to the QTL identified on LG 2, a single additional QTL for SOP was identified on LG 9B (R^2 = 1.31%; Table 2). MIM also identified a dominant × additive epistatic interaction between the *eg* locus (M-QTL LG 2, 57.7) and the QTL on LG 9B (Table 2; Fig. 5). In the normal seed background, the QTL on LG 9B has a small effect on the SOP, but in the egusi background, the homozygous-recessive genotype has lower SOP than the heterozygous and homozygous-dominant genotype (Fig. 5). The effect of the interaction in the overall population is small (R^2 = 0.7%).

To our knowledge this is the first effort to map QTL associated with SOP in Cucurbitaceae. In other oil crops, SOP has been found to be controlled by many genes and numerous QTLs associated with the trait have been identified in soybean, oilseed rape (*Brassica napus*), maize (*Zea mays*), sunflower, etc. (Vollmann and Rajcan, 2010). Epistatic interactions between QTLs associated with SOP have been described in cruciferous (*Brassica* sp.) oil crops (Delourme et al., 2006; Mahmood et al., 2006; Zhao et al., 2005), soybean (Lark et al., 1994), and oats [*Avena sativa* (Zhu et al., 2004)].

We have mapped the location of the *eg* locus in watermelon and identified M-QTL and E-QTL associated with SOP in watermelon. Future research will aim to add markers to LG 2 to tease out potential QTL in addition to the *eg* locus as well as make eventual cloning of the *eg* gene possible. Jarret and Levy (2012) recently reported a high correlation between the hull/kernel ratio and SOP in watermelon, showing that egusi seed has a significantly lower hull/kernel ratio than normal seed. We are currently pursuing this line of research as well as the potential contribution of the paternal genotype to SOP.

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