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Inheritance of Long Husk Leaves of Maize in Recombinant Inbred lines (RILs)

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Husk leaves, surround and usually tightly enclose leaf sheaths, resulted in increase of yield production. Relative frequency distributions of visual husk leaves ratings on Hawaii M Set showed that most populations were skewed toward the lower values in the winter trial (2002) as well as in the spring trial (2003). Recombinant inbred lines (RILs) of Hawaii M Set were derived from inbred Hi38c1(bt) and Ia453 and the visual score ratings of husk leaves of their parents, Hi38c1(bt) and Ia453, were averaged 1.18 and 5.81, respectively.

The visual score ratings of husk leaves for the RILs were ranged from 1.0 to 7.5 with average of 2.15. The length of husk leaf of the first ear showed positive correlation with that of second ear ($r=0.85$, $P<0.01$). The number of tiller showed high correlation with the length of husk leaves in RILs of Hawaii M Set ($r=0.45$, $P<0.01$). Most of the RILs possessed characteristics of long husk leaves (*hls*), prolificacy as well as tiller characters.

Breeding for maize with *hls* and/or tillering appear to hold promise for improving silage maize yield, and especially sweet corn of *hls* is useful for remove husk leaves prior to canning.

INTRODUCTION

The major contribution part of corn production is from leaves to the main stalk. However, in certain genotypes, some leaves may be extended from the modified leaf sheaths or husks surrounding the ear of maize. These leaves are referred to as “husk leaves” and they can significantly add potential photosynthetic products to the corn plant. They may be more efficient in the amount of photosynthates translocated to the kernels than other leaves. Most of tillering plant, grassy tillers (*gt*) and tillered (*tlr*) mutant, have long husk leaves, and their characters contribute to somewhat for crop production. Especially *gt* mutant have many tillers and long husk leaves (*hls*) but corn grass (*cg*) mutant have narrow waxy leaves and vegetative transformed ears and tassels.

Singleton (1949) has suggested that the ancestral form of modern corn is “corn grass”. This anomalous type, the product of a single dominant gene, produces numerous tillers and small “ears” with a high proportion of single spikelet. A few researchers have studied the prospects for development of maize hybrids with multi-tillers and ears (MET). In order to improve the biological yield of modern maize hybrids, a different breeding approach has been attempted using land races with multi-tiller and ear habits (Choe *et al.*, 1982, MNL 56:62). Toward the breeding of a new type of maize hybrid with MET, a few inbred lines with MET were developed and found that this tiller linked to *umc 76* on the short of chromosome 1 (Lee *et al.*, 1995). Jang *et al.* (2004)

cloned and characterized two genes (*ZmRPS4*, *ZmMET1*) that were strongly expressed in tiller base in MET.

Few have been reported on the genetics related to the presence of husk leaf and its length adapted for the Corn Belt Germplasm. Excess leaf tissue in the form of husk leaves may be somewhat analogous to excess glum and awn tissue in some cereal crops. In studies involving isogenic lines of barley, Qualset *et al.* (1965) showed that full and half-awned lines produced higher grain yields than quarter-awned and awnless lines. They reported that awns on a full-awned type contributed 19% of total grain yield.

Rasmusson and Crookston (1977) demonstrated that multiple-awn barley lines produced lower grain yield than normal awn barley lines. Jain (1971) found that 15% of the grain dry matter in a genotype could be attributed to the photosynthesis in the husk leaves. Sawada *et al.* (1994) demonstrated that the efficient contribution on grain production of husk leaves was not due to the photosynthetic rate of their leaves but to the efficient translocation of photosynthesis from them to ear. Because of the proximity of husk leaves to the ear, which is a major sink of photosynthates, the translocation of photosynthates from husk leaves to ear is more efficient than that from culm leaves.

The husk leaves comprise a small percentage of the total plant leaf area. But they may be beneficial in hybrid seed corn production fields where mechanical detasseling often remove a substantial amount of upper-leaf. The yield losses of the seed parent inbred have been estimated to be as much as 28% for the removal of three leaves along with the tassel. The amount of light intercepted by the husk leaves would increase and they may partially compensate for the reduced yield. Cantrell and Geadelman (1981) reported that for dent corn variety, even when husk leaves accounted for as much as 20% of an ear leaf, the decrease in grain yield by husk leaf

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removal was only about 2.6%. Allison and Watson (1996) stated that the contribution of the husk leaves to photosynthesis was negligible under normal conditions but photosynthetic rate increased upon partial defoliation at the time of silking. Literatures on the genetics of this traits conferred by the husk leaves are spare.

The objective of our study was to know (1) frequency distributions of the length of husk leaves (2) the relationship between the husk leaves of the first- and the second-ear and (3) the relationship between husk leaves and tiller characters for 44 Recombinant Inbred Lines (RILs) of Hawaii M Set in sweet corn.

MATERIALS AND METHODS

Plant materials

Hawaii M Set of Recombinant Inbred Lines (RILs) was derived from the cross of inbreds Hi38c1(bt) and Ia453. Parent Hi38c1 is a conversion to *brittle-1* allele of the *sugary-1* inbred Hawaii AA8 and has non-husk leaves. A tropical inbred Ia453, Iowa inbred, is a conversion of the *sugary-1* parent of the popular hybrids "Iochief" and has *hls* and one or two tillers.

The procedure applied to develop RILs was the same as single-seed descent procedure based on the principle that only one seed (line) from each plant is used to advance to next generation in the absence of selection. The lines (ears) in the S₆ generation were planted separately in row (one line per row) and then ten plants in each row (line) were sib-pollinated to produce seeds for the experiment in spring of 2002.

The Hawaii M Set and parents were planted twice on September 5, 2002 (trial 1) and February 27, 2003 (trial

2) in Randomized Complete Block Design (RCBD) with drip irrigation at Waimanalo Research Station, University of Hawaii on Oahu at 21 °N latitude and 30 m elevations. In each trial, each line was planted in each row (24 plants per 2.5 m row with 0.75 m between-row spacing) with 3 replications.

Measurement methods

Husk leaves of the primary ear were visually scored for each of five plants per Hawaii M Set line on a scale of 1 to 9, with 1 indicating no visible husk leaves (less than 1 cm), 2 indicating from 1 to 3 cm, 3 indicating from 3 to 5 cm, 4 indicating from 5 to 7 cm, 5 indicating from 7 to 9 cm, 6 indicating from 9 to 11 cm, 7 indicating from 11 to 13 cm, 8 indicating from 13 to 15 cm, and 9 indicating very long husk leaves (more than 15 cm) at approximately three weeks after silking (Fig. 1). Frequency distributions of the visual scores of husk leaves were computed for all at two seasons. We also used another method to evaluate the length of husk leaves *hls*. Husk leaves of the first- and the second-ear measured with a ruler for each of five plants per Hawaii M Set line.

RESULTS AND DISCUSSION

The average visual score ratings of husk leaves for the parents, Hi38c1(bt) and Ia453 were 1.18 (CV=33%) and 5.81 (CV=34%), respectively (Table 1). RILs were derived from inbred Hi38c1(bt) and Ia453 that typify the difference between non-husk leaves and *hls*. The average visual score ratings of husk leaves for 44 RILs of Hawaii M Set were 2.15, ranging from 1.0 to 7.5.

The visual score ratings of husk leaves of 44 RILs from Hawaii M Set during two year trials (2002 and 2003) were shown in Table 2. Among total 1982 sampled plants, there were 1544 plants (77.9%) with short husk leaves and 438 plants (22.1%) with *hls*.

Days after silking (DTS) and days after anther (DTA) of Hi38c1(bt) were shorter than those of Ia453, and 100 kernel weight was a little lighter in Ia453 (8.5±0.56 g) than in Hi38c1 (10.62±0.54 g), and ear length was somewhat longer in Hi38c1(bt) (20.24±1.31 cm) than in Ia453 (18.74±1.15 cm).

The data on husk leaf-length of the first ear showed



Fig. 1. Husk leaves of RILs of Hawaii M Set.

Table 1. Means and standard deviations of parental inbred, Hi38c1(bt) and Ia453, and 44 RILs of Hawaii M Set, ranges of RIL populations for visual score ratings of husk leaves

Parameter	Visual score rating (1–9)†		
	2002	2003	AVG
Hi38c1(bt)	1.11±0.32*	1.25±0.43	1.18±0.38
Ia453	5.54±1.98	6.07±1.93	5.8±1.96
RILs	2.31±1.51	1.98±1.30	2.15±1.41
Range of RILs	1.0–6.0	1.0–9.0	1.0–7.5

†; Visual score rating (1–9): 1=non-husk leaves (less than 1 cm), 2=1 to 3 cm, 3=3 to 5 cm, 4=5 to 7 cm, 5=7 to 9 cm, 6= 9 to 11 cm, 7= 11 to 13 cm, 8= 13 to 15 cm, 9=more than 15 cm. *: Mean ± SD

Table 2. The visual score ratings and types of husk leaves for Hawaii M Set on Nov. 21, 2002 and May 12, 2003

	1	2	3	4	5	6	7	8	9 [‡]	Mean±SD	HLT
M1	22 [@] (14 [‡])	5	1							1.17±0.52	–
M3	22(9)	5(9)	1	1						1.41±1.93	N
M5	12(12)	7(8)	2							1.39±0.68	N
M6	2(4)	11(9)	7(5)	2(2)	2					1.70±1.06	N
M9	4	10(13)	6(3)	3(4)						1.88±0.93	M
M12	10(11)	13(9)	3							1.48±0.61	W
M13	13(13)	9(4)	3(1)	1	1					1.42±1.81	–
M14	22(15)	3(5)	1							1.22±0.80	N
M15	17(14)	8(5)	1							1.33±0.52	N
M16	10(3)	15(12)	2(4)	1						1.57±0.70	N
M17	1(1)	12(10)	6(7)	2						1.46±0.67	N
M18		9(6)	6(5)	1(4)	5					2.17±0.84	N
M19	27(7)	2(6)	3	3	1					1.43±1.00	–
M21	24(14)	6								1.23±0.34	–
M22	5	13(7)	5(5)	1(8)						1.91±0.92	N
M23	1(3)	2(2)	2(1)	9(2)	8(1)	(2)	3	1(1)	(8)	4.89±2.50	M
M24		(7)	(9)	(4)	2					1.95±0.95	M
M25	24(13)	2(7)								1.26±0.40	–
M26	11(6)	11(7)	2(5)	2(2)						1.57±0.94	W
M27	4	6(7)	7(7)	4(6)	3					2.00±1.08	N
M28	10(8)	6(9)	6(1)	1(1)	2(1)					1.64±1.16	N
M29	9(12)	8(6)	3(1)	2(1)						1.52±0.91	M
M30	10(7)	11(2)	4(1)	3(5)	3	2				2.19±1.48	M
M32	18(6)	8(7)	3(4)	3						1.41±0.91	N
M33	13(5)	6(7)	3(2)	4(6)						1.89±1.17	M
M35	4	5(8)	6(5)	5(7)						2.03±0.98	W
M36	3	6	11	4(4)	(11)	(4)	(1)			3.09±1.42	M
M38	(13)	9(7)	13							1.14±0.79	M
M39			10	12(5)	(4)	(3)	(1)	(3)	(4)	4.19±1.93	M
M41	22(6)	2(11)	1(1)	(1)	(1)					1.47±0.69	–
M42	2(3)	6(7)	6(4)	2(1)	1(1)	(4)				2.16±1.48	N
M43					(6)	(11)	(3)		4	6.50±0.67	N
M45	11(18)	2(2)		1		1				1.43±1.03	M
M48	18(1)	10(8)	(5)	(6)						1.71±1.01	N
M50	13(8)	7(11)	4(1)							1.36±0.65	N
M51	1(5)	5(3)	4(4)	7(5)	2(3)		1			2.63±1.29	N
M53	17(11)	4(8)	2(1)							1.28±0.62	–
M54	(9)	2(4)	4(5)	8(2)	6	2				2.52±1.51	W
M56	(2)	(1)		1(9)	8(4)	9(2)	1(2)			4.97±1.39	M
M57		(2)	8(7)	16(5)	2(2)	4				2.93±0.96	M
M61	23(6)	4								1.16±0.33	–
M62	19(14)	6(4)	2		1(1)	(1)				1.50±1.12	M
M64	(4)	4(4)	4(5)	5(6)	6(1)					2.62±1.26	N
M66	1(1)	(4)	2(5)	5(7)	3(3)	1				3.03±1.21	N
Hi38c1	18(22)	1(4)								1.18±0.31	M
Ia453				(1)	9(11)	13(10)	5(2)	1		5.81±0.78	M
Total	767	519	258	213	115	69	19	6	16		

#: winter trial (2002). @: spring trial (2003). ‡: visual score rating of husk leaves (1= less than 1 cm, 2= from 1 to 3 cm, 3= from 3 to 5 cm, 4= from 5 to 7 cm, 5= from 7 to 9 cm, 6= from 9 to 11 cm, 7= from 11 to 13 cm, 8= from 13 to 15 cm, 9= more than 15 cm). HLT: husk leaf type, N: narrow husk leaves (less 5.5 cm), M: medium husk leaves (between 5.5 and 9.5 cm), W: wide husk leaves (more than 9.5 cm).

positive correlation with those of the second ear ($r=0.85$, $P<0.01$) (Fig. 2). We could find that these husk leaves affects each other, and most of 44 RILs from Hawaii M Set had characteristics of multiple ears or prolificacy (possess more than one ear per plant in each line).

High relationship between tiller number and length of husk leaves in the RILs of Hawaii M Set ($r=0.68$, $P<0.01$) was shown in the Fig. 3. This result indicated that plant with *hls* is likely to have tillering characteristics. Although tillering has been a teosinte-specific character, it has been affected by environment. That could

explain for the tillering of the maize inbred used here even they were non-tillering (single main culm). Although the frequency distribution of the husk leaf-length of the first ear on RILs population of Hawaii M Set had small difference from normality (Fig. 4), departing notably for values from 0 to 2 cm (higher than expected one). In general, there was generally a bell-shaped normal distribution. Most of the husk leaf-length of the first ear were longer than those of the second ear. That means the husk leaf-length of the second-ear depends on those of the first-ear but these data didn't always

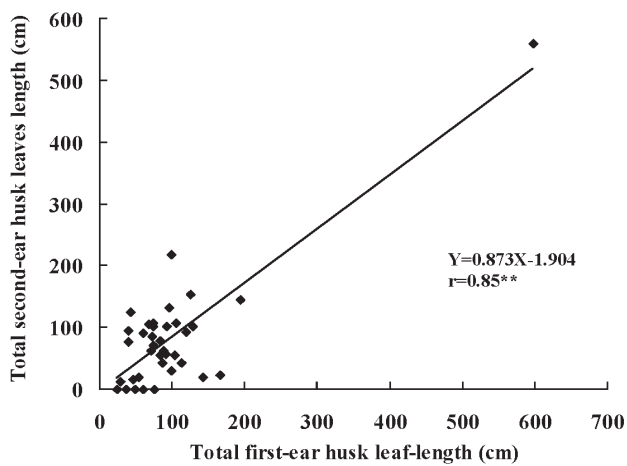


Fig. 2. The relationship between the husk leaf-length of the first- and the second-ear in 44 RILs of Hawaii M Set. **: significant at $P < 0.01$.

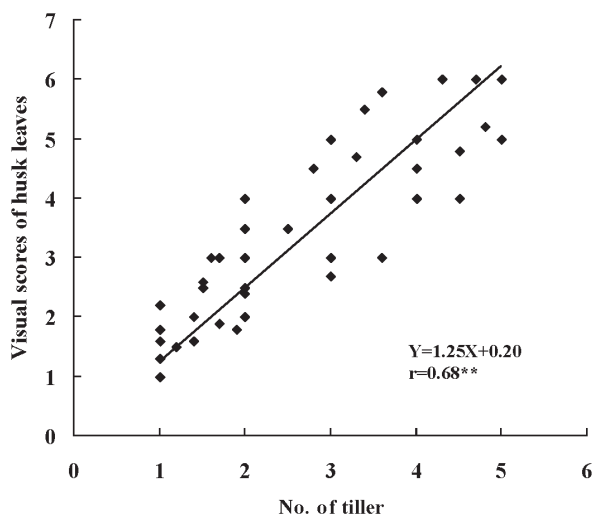


Fig. 3. The relationship between tiller number and husk leaves in 44 RIL populations of Hawaii M Set. **: significant at $P < 0.01$.

showed the same relationship. The husk leaf-length of the second-ear sometimes appeared much longer than those of the first-ear. Because the husk leaf length of the first-ear has an apical dominance in F_1 hybrids but those of the second-ear differ from the husk leaf-length of the first-ear. Most of the second-ear appeared well their characteristics due to affects less the first-ear as like apical dominance. Environment effect plays a major role in expression of tillering as well as husk-leaf length. The length of husk leaves vary depending upon environmental conditions such as growing space, light incident levels, temperature and day length. Field and tropical sweet corn is generally non-tillering (produces one main stem). The frequency distributions of the husk leaf-length on 44 RILs population of Hawaii M Set in combined data during two year trials was skewed towards non-husk leaves type showed in Fig. 4

The husk leaves showed three types (narrow, medium and wide) and the number of RILs be narrow, medium and wide type were 19, 15 and 4, respectively (Table 2). These types of husk leaves appeared either erect ear ecotype with efficient translocation of photosynthate or horizontal ear type.

The plant having *hls* is very useful character in harvest process as well as photosynthesis, and contribute greatly to grain production (Cantrell and Geadelmann, 1981b), and the plants having this character are usually accompanied tillering and prolificacy. The husk leaves of RILs of Hawaii M Set segregated wide range (1 to 9), and showed highly correlated with tillering and prolificacy. The plants in spring trial showed more *hls* characters than those in the winter trial. The husk leaves of the second-ear depended on those of the first-ear. However, for some RILs of Hawaii M Set has no husk leaves, the second-ear still showed *hls*. The husk leaves evaluation of RILs in this study showed *hls* was transferable by backcrossing. Breeding programs for *hls* also considered prolificacy and tillering, because in most of the cases, those characters seem to act together and have influence on each other.

Simple selection method with high potential to

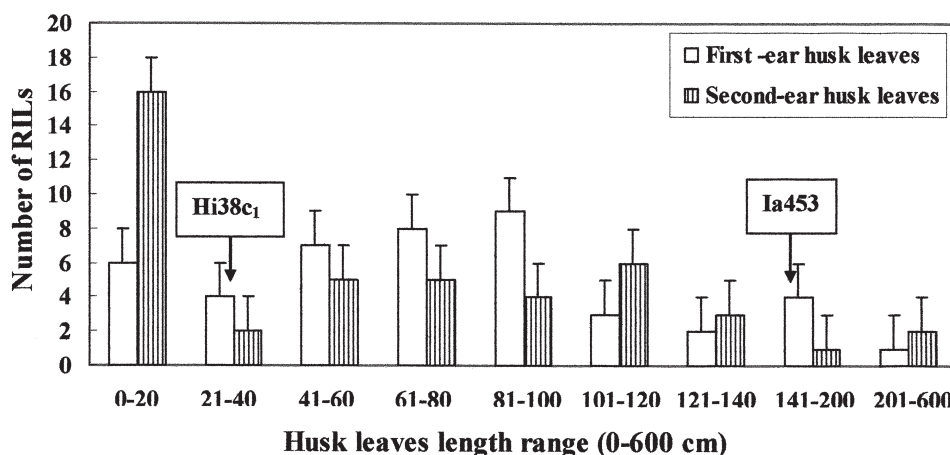


Fig. 4. Frequency distribution of the husk leaves length between the first- and the second-ear on RIL populations of Hawaii M Set.

accelerate breeding progress for husk leaves in maize will gain wide acceptance if it can be economically competitive with present breeding methods. The study on tiller and husk leaves was still received less attention compared to that of other characteristics, and they have been studied separately. The husk leaves of RILs of Hawaii M Set showed three leaf types (narrow, medium and wide), and depend on their genetic background.

Most studies on husk leaves focused on yield contribution rather than basically genetic aspects. Sawada *et al.* (1995) demonstrated that the high efficiency of grain production of husk leaves was not due to the photosynthetic rate of leaves but to the efficient translocation of photosynthates from these leaves to ear. They explained that because of the proximity of husk leaves to the ear, which is a major sink of photosynthates, the translocation of photosynthates from husk leaves to ear is more efficient than that from culm leaves. It is well known that the photosynthesis of leaves on the main culm of corn is the C₄ type. However, the husk leaves is reported to be C₃-C₄ intermediated type in terms of photorespiration rate (Langdale *et al.*, 1988).

Maize tillering is one of the plant characteristics that have been neglected and unwanted for breeding purpose. However, it has been continued the studies on some tillering maize (Lee and Choe, 1988, 1991; Choe *et al.*, 1989, 1992; Lee *et al.*, 1994; Ji and Choe, 1998a, 1998b, 1999), because those tillering maize are quite different from other general tillering maize reported by Neuffer and Hoisington (1987). The tillering is claimed to be not monogenic but multigenic and temperature dependent (Choe and Lee, 1991; Choe *et al.*, 1993) and some of tillering hybrids produced greater dry matter than leading U. S. maize hybrids, non-tillering maize (Choe *et al.*, 1998). Choe and Han (1984) reported that the tillering of the MET line had the cytoplasmic effects on the number of tillers and ears in Korea.

According to other tillering type maize, the maturing embryo is the only totipotent meristem that is produced during the life cycle of the plant. The perennialism (*pe*) is maintained because basal branches retain totipotency. The *pe* appeared to act the totipotency of basal branches. It was assumed that it might confirm *pe* to any strongly tillering type of maize. The *gt*, other mutant type of maize, causes the production of numerous small tillers at the base of the main culm that terminate in small female inflorescences. Shaver (1967) reported a mutant '*gt1*' for grassy tiller, which had numerous branches and showed vegetatively totipotent in combination with '*pe1*' and "*id1*". The mutant "*id1*" standing for indeterminate growth was reported by Singleton (1946).

The Ia453 inbred line with *lhls* showed a prolificacy. Prolificacy maize also appeared tillering character as like *gt*, *cg* and *pe* mutant so on, and showed long shank traits as Ia453 inbred.

NE-EDRsh2, another inbred line with *lhls*, also appeared tillering and *lhls* traits in Hawaii. We could assume that their three traits (tillering, long husk leaves, indeterminate growth) highly correlated with each other

(data not shown) like *gt*, *cg* and *pe* mutant. Firstly, in breeding for maize of *lhls*, we must consider whether prolificacy traits eliminate or not, because these traits always have interaction with each other. Secondly, disadvantage traits, which maize of *lhls* sometimes have tip unfilled, small ear, irregular ear-row characters, long shank, and prolificacy, should be considered for breeding purpose in advance.

Breeding for *lhls* or tillering maize seems to be more advantage for silage production than grain yield increasing. Based on the results from this study, it is expected that tillering and *lhls* play an important role in improving silage maize yield, and especially sweet corn with *lhls* and also be useful for machine-handling prior to canning.

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