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Frequency of the transposable element *Uq* in Iowa stiff stalk synthetic maize populations

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Summary

The *Uq* transposable element is one of two transposable elements consistently found in maize (*Zea mays* L.) populations. Populations developed from two independent recurrent selection programs initiated in the Iowa Stiff Stalk Synthetic (BSSS) maize population were tested for the frequency of *Uq* transposable elements to determine how *Uq* frequency has changed with cycles of recurrent selection. In the first programme, 13 cycles of half-sib and S_2 progeny recurrent selection [BSSS(S)C13] have been completed and 10 of the 13 cycles were assayed for active *Uq* elements. In the second programme, 11 cycles of reciprocal recurrent selection [BSSS(R)C11] have been completed and five of the 11 cycles were assayed for active *Uq* elements. The frequency of *Uq* was different for the two recurrent-selection programmes. The percentage of plants containing active *Uq* elements increased from 19% (BSSS) to 91% [BSSS(S)C13] at a linear rate after 13 cycles of half-sib and S_2 progeny recurrent selection, whereas the percentage of plants containing active *Uq* elements decreased from 19% (BSSS) to 0% [BSSS(R)C11] after 11 cycles of reciprocal recurrent selection, with extinction of the *Uq* element occurring between the fifth and sixth cycles of selection. Our data suggest that the increase in frequency of *Uq* with half-sib and S_2 progeny recurrent selection was predominantly due to random genetic drift coupled with a selective advantage possibly associated with a region of the genome linked to *Uq*. Neither replicative transposition or chromosome assortment and segregation can be invoked to explain the change in frequency of *Uq* in these populations. The extinction of *Uq* after reciprocal recurrent selection was best explained by random genetic drift.

1. Introduction

The Iowa Stiff Stalk Synthetic (BSSS) maize (*Zea mays*, L.) population has made significant contributions to the hybrid-seed maize industry. In a survey conducted by Zuber & Darrah (1980), inbred lines developed from BSSS (B14, B37, B73, B84) were used as a parent in 19% of the total hybrid-seed maize needed to plant the 1980 U.S. maize acreage. This is a minimum estimate of the contribution of BSSS, because it does not include lines related to B14, B37, B73, and B84, and proprietary lines developed from BSSS. BSSS was developed by Sprague (1946) by intermating 16 inbred lines in 1933 and 1934 (Hallauer *et al.* 1983). Since the synthesis of BSSS, BSSS has been used as the base population in two independent recurrent-selection programmes. In the half-sib and S_2 progeny programme, 13 cycles of selection have been completed, and in the reciprocal recurrent selection programme, 11 cycles of selection have been completed.

One of the 16 lines used to form BSSS, Ial159, is known to carry an active *Uq* transposable element (Cormack *et al.* 1988). Peterson (1986) and Peterson & Salamini (1985) screened six of the improved populations of BSSS developed by half-sib and S_2 progeny recurrent selection and found active *Uq* transposable elements in three of them. The inability to detect active *Uq* elements in the other three populations was likely due to small sample sizes. The *Uq* transposable element has persisted in BSSS during several cycles of intense selection for yield and other traits despite the small number of lines that have been intermated with each cycle of selection. BSSS has been a closed population during recurrent selection; in other words, new germplasm has not been introduced into BSSS. Therefore, active *Uq* transposable elements not present in the progenitor lines are not expected to exist in BSSS unless non-active elements have become active spontaneously.

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That element sequences are universally present is not questioned, but the presence of *active Uq* transposable elements in BSSS has lead to the hypothesis that *Uq* may be beneficial to the population by creating new genetic variation that can be selected by maize breeders. Our study is one of a series of experiments designed to determine why and how *Uq* has been maintained during recurrent selection in BSSS and what role *Uq* has had in selection response. This study reports on an experiment designed to determine the changes in frequency of the *Uq* transposable element in two independent recurrent-selection programmes.

2. Materials and methods

Recurrent selection (Hallauer, 1985) is a cyclical selection procedure that involves three phases conducted in sequence (Fig. 1): (1) development of progenies (half-sibs, S_1 lines, S_2 lines, etc.) (Fig. 2); (2) evaluation of these progenies in replicated experiments so that the top fraction can be selected on the basis of the traits of interest; and (3) intermating of the selected progenies to form a new random mating population in which to initiate the next cycle of selection. The completion of all three phases constitutes one cycle of selection. Each cycle of selection takes from 2 to 4 years depending on the type of progenies evaluated and the availability of a winter nursery. The primary objectives of recurrent selection are to increase the mean performance for the traits of interest and to maintain genetic variation for continued improvement of the population.

The BSSS population was used as the base population in two independent recurrent selection programmes (half-sib followed by S_2 progeny recurrent selection and reciprocal recurrent selection). Half-sib recurrent selection using the double-cross Iowa 13 as the tester was initiated in 1939. A number of plants in BSSS were self-pollinated and each plant was crossed to approximately 10 plants of Iowa 13. At maturity, 167 plants were selected and the corresponding testcross (half-sib) progenies were evaluated in replicated experiments in 1940. The testcross progenies are related as half-sibs through the common parent Iowa 13 (Fig. 2). Ten plants were selected on the basis of their testcross performance and remnant S_1 seed was intermated to produce BSSS(HT)C1. The recurrent selection programme was continued similarly for six additional cycles. The number of individual plants crossed with Iowa 13 (the tester) and included in the evaluation experiment for each cycle of selection is given in Table 1. Details of the experimental procedures used for the seven cycles of half-sib recurrent selection were described by Eberhart *et al.* (1973).

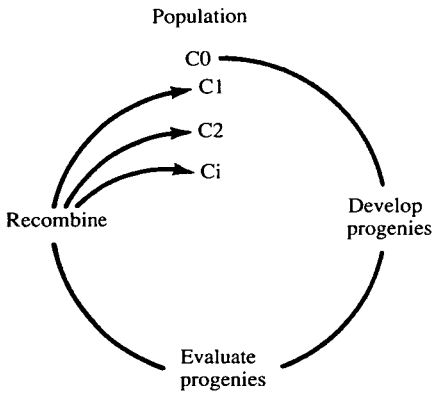

Fig. 1. The cyclical nature of recurrent selection, showing the development of progenies, the evaluation and selection of superior progenies from replicated experiments, and the recombination (intermating) of selected progenies to form a new cycle of selection. Recurrent selection methods differ in the type of progenies that are evaluated. Half-sib and S_2 progeny recurrent selection and reciprocal recurrent selection initiated in BSSS in 1939 and 1949, respectively, involved all three phases outlined in the figure. (Modified from Hallauer, 1985).

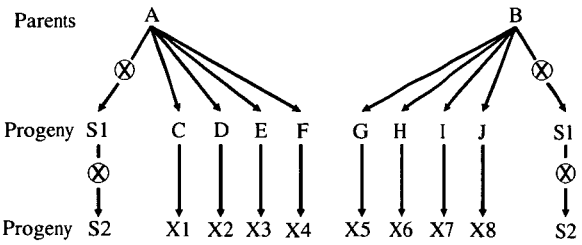

Fig. 2. An illustration of how S_2 and half-sib progenies are generated in recurrent selection. Parents A and B are unrelated, non-inbred plants from a base population such as BSSS. Plants C to F and G to J are sampled from a tester population (in the half-sib and reciprocal recurrent selection programs in BSSS these plants would be from Iowa 13 and BSCB1(R)Cn, respectively). The progeny from the four crosses (X1 to X4 or X5 to X8) are then bulked together to form a half-sib family that is evaluated in replicated experiments so that the top fraction of progenies can be selected on the basis of the traits of interest. S_2 progenies are developed in the following way: plants A or B are selfed to develop S_1 progenies and then a single plant within the S_1 progeny is selfed to obtain an S_2 progeny. In the first cycle of S_2 progeny recurrent selection, plants A and B were sampled from BSSS(HT)C7.

After the completion of seven cycles of half-sib selection, the selection method was changed to S_2 progeny recurrent selection beginning with the sampling of BSSS(HT)C7 (Hallauer *et al.* 1983). S_2 progenies were developed by selfing a number of individual plants in BSSS(HT)C7 (Fig. 2). The resulting S_1 progenies were then grown in the nursery, and one plant within each S_1 progeny was selfed to produce an S_2 progeny (Fig. 2). At maturity, 100 S_1 progenies were selected and the corresponding S_2 progenies were evaluated in replicated experiments in 1972. Ten S_2 progenies were selected based on their performance and remnant S_2 seed was intermated to produce BSSS(S)C8. The recurrent selection programme was continued similarly for five additional

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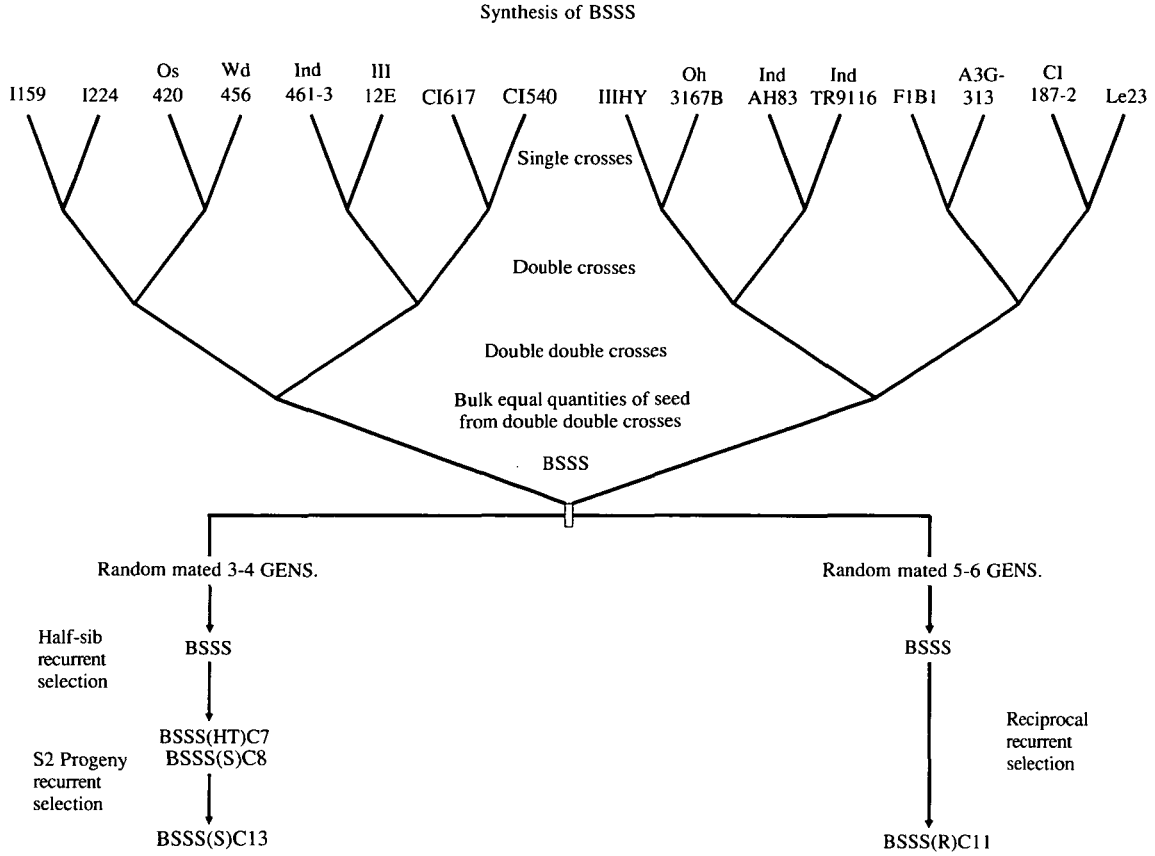

Fig. 3. The development of BSSS and populations derived from BSSS by recurrent selection. The original crosses that were made to develop BSSS are shown along with half-sib and S_2 progeny recurrent selection (*a*) and reciprocal recurrent selection (*b*) that were started by using BSSS as the base population. The method of progeny development for half-sibs, S_2 progeny, and reciprocal recurrent selection are described in the text. Random mating is a crossing procedure done by hand or in isolation that ensures that each individual has an equal chance of mating with any other individual in the population. (Modified from Lee, 1989).

cycles, except that remnant S_1 seed was intermated from cycles 10 to 12. The number of S_2 progenies evaluated in each cycle of selection is given in Table 1. The first seven cycles of half-sib recurrent selection have been designated BSSS to BSSS(HT)C7, and the last six cycles of S_2 progeny recurrent selection have been designated BSSS(S)C8 to BSSS(S)C13 (Fig. 3*a*). This recurrent selection programme will be referred to as 'half-sib and S_2 progeny recurrent selection'.

Reciprical recurrent selection using the BSCB1(R)Cn population as the tester was initiated in BSSS in 1949 (Fig. 3). A number of plants in BSSS were self-pollinated and each plant was crossed to approximately 10 plants of the BSCB1 tester population. At maturity, 99 plants were selected and the corresponding testcross (half-sib) progenies were evaluated in replicated experiments in 1950. A similar procedure was followed to obtain self-pollinations and testcrosses in BSCB1. Ten plants from each population were selected based on testcross performance and remnant S_1 seed was intermated to produce BSSS(R)C1 and BSCB1(R)C1. The reciprocal recurrent selection programme was conducted similarly for eight additional cycles. For the last two cycles of selection (C10 and C11) the type of progenies evaluated was changed from half-sibs to full-sibs. Details of the methods for conducting reciprocal recurrent selection in BSSS were given by Penny & Eberhart (1971). The populations resulting from 11 cycles of reciprocal recurrent selection have been designated BSSS to BSSS(R)C11 (Fig. 3*b*).

Active *Uq* transposable elements were detected in each of the sampled populations by using the *c-ruq* *m*obile *e*lement *r*eceptor *l*ine (MERL). This MERL is a line that contains a receptor element (non-autonomous) for the regulatory (autonomous) *Uq* element inserted in the *C* gene. When inserted into the *C* gene, the receptor element suppresses the function of the *C* gene (purple aleurone) and results in colourless kernels. Lines homozygous for *c-ruq* will have colourless kernels unless an active *Uq* is present in the genome in which case the kernels will have coloured spots (excision events) on a colourless background. This assay is a rapid, simple, and accurate way to detect active *Uq* elements in individual plants (Figure 4).

The populations screened for active *Uq* elements are listed in Tables 1 and 3. The population was used as a female in all crosses with the MERL except for BSSS(S)C11, which was used as a male. All pollina-

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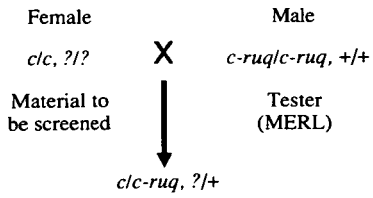

Fig. 4. Crossing scheme used to test for the presence of active *Uq* elements within individual plants contained in a population. The female plants are being tested for active *Uq* elements and the males are known to lack active *Uq* elements. A question mark implies that the *Uq* content of each plant was unknown at the time of the test; a '+' indicates no active *Uq* is present. If the female plant contains an active *Uq* element, the progeny of the cross will segregate for colourless and spotted kernels. If the female plant lacks an active *Uq* element the progeny of the cross will lack spots on all colourless kernels.

tions were made by hand. If an ear had kernels containing coloured spots on a colourless background, the plant from the population that produced that ear was scored as containing at least one copy of an active *Uq* element. Ears without spotted kernels and containing fewer than 33 kernels were discarded to minimize the risk of scoring a plant as lacking active *Uq* elements due to unintentional outcrossing and small sample size. The percentage of plants containing *Uq* and the allelic frequency of *Uq* were calculated by using this data. The percentage of plants containing *Uq* was calculated as the ratio of the number of plants scored as containing at least one copy of *Uq* to the total number of plants screened. The allelic frequency of *Uq* was calculated as $1-\sqrt{(n/N)}$, where n is the number of plants lacking *Uq* activity and N is the total number of plants screened. The standard error of the allelic frequency of *Uq* was calculated as $\sqrt{((N-n)/4N^2)}$. The *Uq* allelic frequency is a maximum likelihood estimate; it assumes *Uq* segregates as a Mendelian gene and assumes all *Uq* elements present in the genome are allelic.

The percentage of spotted kernels per plants was calculated as the ratio of the number of spotted kernels to total kernel number times 100 for the half-sib and S_2 recurrent selection program. These values were then averaged over plants with spotted kernels within each population to obtain the mean percentage of spotted kernels per plant. The mean was used as a relative measure of the abundance of *Uq* elements per plant within each population. A lower limit of the mean was calculated by making the same assumptions used to calculate *Uq* allelic frequency. Letting p be the allelic frequency of *Uq*, then the lower limit of the mean is $p/p(2-p)*100$. Estimates of p obtained from the data were used in the equation.

3. Results

(i) *Half-sib and S_2 progeny recurrent selection*

Data for the 13 cycles of half-sib and S_2 progeny recurrent selection are presented in Table 1. The number of testcross progeny evaluated ranged from 86 to 167 for the first seven cycles, and the best 10 of these were selected and intermated. Selection intensity ranged from 6·0 to 11·6%. For the six cycles of S_2 recurrent selection, 100 to 150 S_2 progenies were evaluated and 10 or 20 were selected and intermated. Selection intensities ranged from 10·0 to 20·0%. The increase from selecting 10 progenies to selecting 20 progenies occurred after two cycles of S_2 selection; the change was made to reduce the possible deleterious

Table 1. *Selection data from seven cycles of half-sib recurrent selection, followed by six cycles of S_2 progeny recurrent selection, and the results of screening these populations for the* Uq *transposable element system*

	Selection data				Transposable element data		
Population	Cycle of selection	Number of progeny evaluated	Number of progeny selected	Percentage of progeny selected	Number of plants screened	Percentage of plants containing *Uq*	Frequency of *Uq*
BSSS	0†	167	10	6·0	67	19±4·8	0·10±0·03
BSSS(HT)	1	167	10	6·0	—	—	—
BSSS(HT)	2†	108	10	9·3	61	25±5·5	0·13±0·03
BSSS(HT)	3	88	10	11·4	—	—	—
BSSS(HT)	4†	91	10	11·0	58	36±6·3	0·20±0·04
BSSS(HT)	5	86	10	11·6	—	—	—
BSSS(HT)	6†	90	10	11·1	68	51±6·1	0·30±0·04
BSSS(HT)	7†	100	10	10·0	74	51±5·8	0·30±0·04
BSSS(S)	8†	100	10	10·0	85	46±5·4	0·26±0·04
BSSS(S)	9†	100	20	20·0	74	74±5·1	0·49±0·05
BSSS(S)	10	100	20	20·0	—	—	—
BSSS(S)	11†	100	20	20·0	69	80±4·8	0·55±0·05
BSSS(S)	12†	150	20	13·3	207	79±2·8	0·54±0·03
BSSS(S)	13†	—	—	—	160	91±2·3	0·69±0·04

† Populations sampled for active *Uq* transposable elements.

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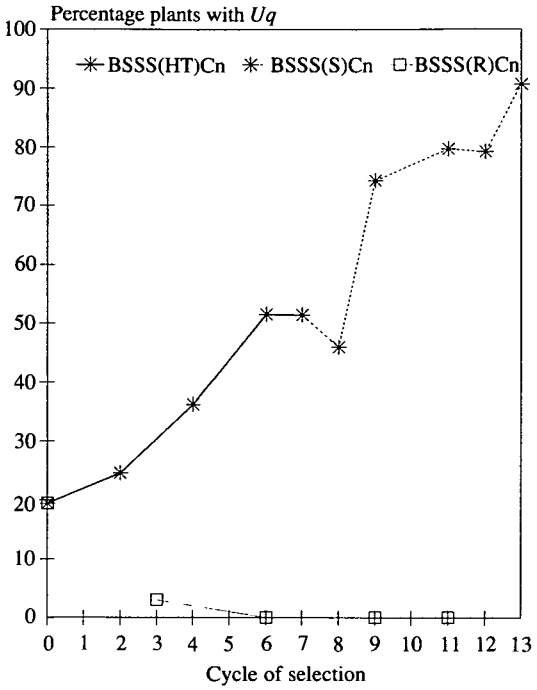

Fig. 5. Plot of the percentage of plants containing an active *Uq* element in each cycle of half-sib and S_2 progeny recurrent selection, and reciprocal recurrent selection in BSSS.

(inbreeding depression and reduced genetic variance) effects of selecting only 10 progenies. The primary trait under selection has been grain yield, with selection pressure on less grain moisture at harvest and resistance to stalk lodging and root lodging.

All but four of the 14 populations resulting from 13 cycles of selection were screened for active *Uq* transposable elements (Table 1). The number of plants screened in each population ranged from 58 to 207. The percentage of plants containing active *Uq* elements increased from 19 in BSSS to 91 in BSSS(S)C13. The increase in percentage of plants containing active *Uq* elements was linear ($R^2 = 0{\cdot}94$) and occurred at a rate of 5·6% per cycle of selection (Fig. 5). As expected, the allelic frequency of *Uq* showed a linear trend similar to that for percentage of plants containing active *Uq* elements (Table 1). There was no apparent effect of method of recurrent selection (half-sib vs. S_2) on the increase in the frequency of plants containing active *Uq* elements. The major deviations from regression occurred with the cycle 8 and cycle 9 populations. The cause of these deviations is unknown.

The distributions of percentage of spotted kernels per plant within each population are shown in Table 2. The majority of the plants for all populations fell in the range of 30 to 60% spotted kernels per ear. Plants with fewer than 50% spotted kernels are not expected theoretically, but these plants may arise experimentally for several reasons. The most likely reason is sampling, however unintentional outcrossing by not providing a reporter allele and a low activity *Uq* element may also cause a deficiency of spotted kernels. The large number of plants in BSSS(S)C12 with fewer than 50% spotted kernels is probably due to the low dosage of *Uq* in the endosperm from crossing plants in the population as males to the MERL as females. The activity of the *Uq* element has been shown to be dosage dependent (Peterson, 1987). Plants with more than 50% spotted kernels are expected theoretically, but we do not have enough data to reliably determine genetically the cause of these plants. The mean percentage spotted kernels per plant ranged from 46·9 to 65·4%. The mean was less than the expected lower limit for all populations.

(ii) *Reciprocal recurrent selection*

The number of progenies evaluated per cycle ranged from 90 to 125 and the best 10 or 20 of these were selected for recombination (Table 3). Selection intensities ranged from 9·7 to 20%. The primary trait under selection has been yield, with selection pressure

Table 2. *Distribution and mean of the percentage spotted kernels per plant for populations screened for active* Uq *transposable elements from the half-sib and S_2 recurrent selection programme*

Population	Spotted kernels (%) 5	15	25	35	45	55	65	75	85	95	N†	Mean	Expected Lower Limit‡
BSSS	0	1	0	3	5	0	1	1	1	1	13	51·3	52·6
BSSS(HT)C2	0	0	1	2	8	3	0	0	0	1	15	47·2	54·0
BSSS(HT)C4	0	0	1	3	11	4	0	0	1	1	21	49·3	55·6
BSSS(HT)C6	0	1	2	5	15	6	1	1	1	3	35	50·3	58·8
BSSS(HT)C7	0	1	3	2	17	7	2	0	0	6	38	53·6	58·8
BSSS(S)C8	0	0	0	4	14	12	2	1	2	4	39	55·9	57·8
BSSS(S)C9	1	0	0	9	25	7	1	2	2	8	55	54·4	66·2
BSSS(S)C11	2	2	2	3	14	7	4	6	6	8	54	58·6	68·8
BSSS(S)C12	7	10	23	26	40	12	14	17	11	4	164	46·9	68·4
BSSS(S)C13	2	3	2	12	46	15	4	5	9	47	145	65·4	77·2

† N is the number of plants with active *Uq* elements.
‡ Expected lower limit of the mean assuming all *Uq* elements in the genome are allelic.

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Table 3. *Selection data from 11 cycles of reciprocal recurrent selection and the results of screening these populations for the* Uq *transposable element system*

	Selection data				Transposable element data		
Population	Cycle of selection	Number of progeny evaluated	Number of progeny selected	Percentage of progeny selected	Number of plants screened	Percentage of plants containing *Uq*	Frequency of *Uq*
BSSS	0†	99	10	10·1	67	19±4·8	0·10±0·03
BSSS(R)	1	102	10	9·8	—	—	—
BSSS(R)	2	103	10	9·7	—	—	—
BSSS(R)	3†	101	10	9·9	66	3±2·1	0·02±0·01
BSSS(R)	4	90	10	11·1	—	—	—
BSSS(R)	5	100	10	10·0	—	—	—
BSSS(R)	6†	100	10	10·0	56	0	0·00
BSSS(R)	7	100	10	10·0	—	—	—
BSSS(R)	8	100	20	20·0	—	—	—
BSSS(R)	9†	160	20	12·5	58	0	0·00
BSSS(R)	10	100	20	20·0	—	—	—
BSSS(R)	11†	125	20	16·0	49	0	0·00

† Populations sampled for active *Uq* transposable elements.

on less grain moisture at harvest and resistance to root lodging and stalk lodging.

Five of the 12 populations resulting from 11 cycles of reciprocal recurrent selection were screened for active *Uq* transposable elements (Table 3). The number of plants screened ranged from 49 to 67. The percentage of plants containing active *Uq* elements decreased from 19% in BSSS to 3% in BSSS(R)C3 (Fig. 5). Plants containing active *Uq* elements were not found in the populations sampled after BSSS(R)C3. Cormack *et al.* (1988) reported finding active *Uq* elements in BSSS(R)C5 but did not find them in BSSS(R)C1 or BSSS(R)C10. These data suggest the loss of active *Uq* elements occurred between the sampling of BSSS(R)C5 and the formation of BSSS(R)C6. The failure of Cormack *et al.* (1988) to detect *Uq* in BSSS(R)C1 was likely due to the small number of plants tested from the population.

4. Discussion

Populations developed from two independent recurrent-selection programmes in the same base population (BSSS) were tested for their *Uq* content to determine how *Uq* frequency changed with cycles of recurrent selection. The two recurrent-selection programmes produced different results. The percentage of plants containing active *Uq* elements increased linearly from 19% in BSSS to 91% in BSSS(S)C13 (Fig. 5), whereas the percentage of plants containing active *Uq* elements decreased from 19% in BSSS to 0% in BSSS(R)C11 with extinction of the element occurring between the fifth and sixth cycles of selection (Fig. 5). The populations in both recurrent selection programmes have been closed during recurrent selection meaning that germplasm external to the populations has not been introduced into the populations. Therefore, the addition of external germplasm cannot be used to explain the changes in *Uq* content of the populations.

The most reasonable explanation for the increase in *Uq* frequency in the half-sib and S_2 recurrent-selection programme is random genetic drift. This was tested by using models described by Schaffer *et al.* (1977) and Wilson (1980). These models are dependent on the variance effective population size and the number of plants sampled to determine allelic frequency. The variance effective population size for each cycle of selection was assumed to be equal to the number of progenies selected for intermating (Vencovsky, 1978). The model assumes that individuals were sampled randomly and independently from random-mating populations. Fitting the model to *Uq* allelic-frequency data requires the additional assumptions that *Uq* is a single copy Mendelian gene and that *Uq* has a low or zero frequency of transposition and excision. Two models were fit to the data. The first model tests whether the observed allelic frequency variation from cycle to cycle was consistent with that predicted from the null hypothesis of drift acting alone. The deviation sums of squares calculated to test this hypothesis has, under the null hypothesis, a central χ^2 distribution with one degree of freedom (df) less than the number of generations observed. This test is sensitive to all departures from drift, but is not particularly sensitive to directional changes in allelic frequency. The power of the test to detect directional changes in allelic frequency is increased by partitioning the deviation sums of squares into a single degree of freedom partition that has a central χ^2 distribution under the null hypothesis, but includes all the effects of any linear trend in allelic frequency (Schaffer *et al.* 1977).

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The χ^2 value for deviations from drift (deviation sums of squares) was 12·16, with 9 degrees of freedom and the χ^2 value for a linear trend was 5·03 for the half-sib and S_2 recurrent-selection program. The deviation sums of squares were not significant ($P < 0{\cdot}05$), suggesting that there were no departures from a model based solely on drift. The linear sums of squares, however, were significant and accounted for 41% of the deviations sum of squares. The significant linear sums of squares suggests an underlying linear trend for *Uq* allelic frequency even though the overall gene frequency changes did not exhibit significant departures from genetic drift. The apparent discrepancy between the two models is due to the greater power of the test for a linear trend (Schaffer *et al.* 1977). Even though the change in *Uq* allelic frequency is linear over cycles, the model does not imply a mechanism for producing this change.

Under the assumption that *Uq* has a low or zero rate of transposition and excision, the simplest model for explaining a directional change in the frequency of *Uq* is direct selection for *Uq*. An alternative, but somewhat analogous explanation, is that *Uq* is tightly linked to a segment of the genome related to the expression of the selection criteria. There is no evidence to support either hypothesis, and the large increase in the frequency of *Uq* would require a large selective advantage to be placed on *Uq* or the region of the genome linked with *Uq*, which may be possible. The assumption of a low or zero rate of transposition and excision is also unsupported. But, since the *Uq/ruq* transposable element system was described (Friedemann & Peterson, 1982) there has been only one report of an *Uq* transpositional event (Pan & Peterson, 1989). The pervasiveness of *Uq* in genetic tester stocks, commercial inbred lines, and populations suggests that transpositional events have occurred in the past (Peterson, 1986; Peterson & Friedemann, 1983; Peterson & Salamini, 1985; Cormack *et al.* 1988).

The linear increase in the percentage of plants containing active *Uq* elements could be due to mechanisms other than directional selection such as replicative transposition. Replicative transposition is a model that postulates that transposable elements replicate in the transposition process such that they remain at their original site while moving to new sites (Shapiro, 1979). An alternative model of transposition is the 'cut-and-paste' model where transposition occurs by excision of the transposable element from one position in the genome and re-insertion of the same element at another site (Saedler & Nevers, 1985). The cut-and-paste model of Saedler & Nevers (1985) is thought to be the predominant mode of transposition of maize transposable elements. Our data do not support replicative transposition as the predominant mode of *Uq* transposition. A model of replicative transposition would predict an increase in the number of nonallelic *Uq* elements per genome with cycles of selection (for a review of the population genetics of transposable elements see Charlesworth, 1988). The data presented in Table 2 suggest that *Uq* element number has been stable over cycles of selection and supports the cut-and-paste model of transposition. The mean percentage spotted kernels was less than the expected lower limit calculated assuming all *Uq* elements in the genome are allelic (Table 2). Therefore, models with multiple copies of *Uq* per genome are not required to explain these data. However, the exact distribution and location of *Uq* elements cannot be determined reliably until a molecular probe becomes available.

The spread of *Uq* through these populations could also be accomplished by chromosome assortment and recombination. Good & Hickey (1987) presented an example where 10% of the individuals in a population each have 50 copies of a transposable element. After three generations, 57% of the individuals in the population would each contain an average of 8·8 transposable elements. This model is characterized by an increase in the frequency of individuals carrying transposable elements and a decrease in the number of elements per individual (Good & Hickey, 1987; Good *et al.* 1989).

BSSS was synthesized from 16 lines (Sprague, 1946) by forming eight single crosses, four double crosses, two double-double crosses, and then bulking equal quantities of seed of the two double-double crosses (Fig. 3). The population was then random mated for three to six generations. This mating procedure ensured that each of the original lines contributed equally to the resulting population. One (Ial159) of the original 16 lines used to form BSSS is known to contain at least one active *Uq* element (Cormack *et al.* 1988). Assuming Ial159 is homozygous for *Uq*, that *Uq* segregates as a normal Mendelian gene, and that the 16 lines that formed the BSSS base population each contributed equally to the population, then the expected frequency of *Uq* in BSSS is 0·0625 (1 out of 16). The observed frequency of 0·11 (Table 1) is nearly double the predicted frequency. The observed frequency is not consistent with the hypothesis that only one of the original 16 lines carried an active *Uq* transposable element. The discrepancy between observed and predicted frequencies may be because two of the original 16 lines used to form BSSS were not recovered (Hallauer *et al.* 1983), and, hence, no direct test of their *Uq* content could be made. The possibility exists that one of these two missing lines may have contained an active *Uq* transposable element allelic to the element contained in Ial159. The discrepancy between observed and predicted frequencies could also be explained if Ial159 was homozygous for two non-allelic independent *Uq* elements or if one of the two non-recovered progenitor lines contained an *Uq* element non-allelic to the *Uq* element contained in Ial159. If this was true, 22% of the plants in the newly formed BSSS would be expected to contain *Uq*

elements through the process of chromosome assortment and segregation. This figure is in close agreement with the observed value of 19% (Table 1). Assuming two non-allelic *Uq* elements were introduced into BSSS via the progenitor lines, the model of chromosome assortment and segregation cannot explain the increase in *Uq* frequency with cycles of selection because BSSS was near equilibrium for unlinked loci when recurrent selection was initiated. The probability that one of the two non-recovered progenitor lines contains an active *Uq* element is small, because only one (IaI159) of 21 inbreds screened by Cormack *et al.* (1988) contained active *Uq* elements. Peterson (1988) has postulated that selection for uniformity and stability during inbred line development may cause active *Uq* elements to disappear from maize inbreds. We are currently conducting the experiment to determine the number of active *Uq* elements in IaI159.

The random-genetic-drift model was also fit to the *Uq* allelic frequency data from reciprocal recurrent selection. The χ^2 value for deviations from drift was 1·98, with 4 degrees of freedom, and the χ^2 value for a linear trend was 0·89. The deviations sums of squares were not significant ($P < 0{\cdot}05$) indicating there were no significant departures from a model based solely on drift. Likewise, the linear sums of squares were non-significant, indicating the absence of directional change in the *Uq* allelic frequency. Therefore, the extinction of *Uq* from the reciprocal recurrent selection populations was likely the result of random genetic drift.

These data present us with an interesting contradiction. With half-sib followed by S_2 recurrent selection, *Uq* has increased in frequency to 91% of the population, whereas, with reciprocal recurrent selection, the element has become extinct. The immediate observation is that the change in *Uq* frequency was dependent on the recurrent-selection method. Testcross (half-sib) progenies were evaluated to identify the superior plants for recombination with both half-sib and reciprocal recurrent selection (Fig. 2). The testers used for both methods were heterogeneous and significant progress from selection has been realized in both programmes, although data from experiments to evaluate progress from selection suggests that the two programmes have been increasing the frequency of alleles at different sets of loci (Hallauer *et al.* 1983). These data raise the possibility that with half-sib recurrent selection a region of the genome linked to *Uq* had a selective advantage whereas with reciprocal recurrent selection this same region of the genome lacked a selective advantage due to masking effects of the tester (Rawlings & Thompson, 1962). S_2 progeny selection following half-sib selection had little apparent effect on the change in *Uq* frequency, which may indicate a continued selective advantage for the region of the genome linked to *Uq*. Additional data are needed to verify the effects of selection on changes in *Uq* frequency as well as evidence that *Uq* has not transposed from its original location in the BSSS base population.

Molecular evidence on the effects of transposon insertion and excision in maize has demonstrated that insertion of a transposon at a gene site adds a specific number of nucleotides to that the gene sequence. The number added depends on the specific transposon system (Peterson, 1987). Excision of the transposon from the gene site almost always alters the gene sequence from the original progenitor form (Sachs *et al.* 1983; Schwarz-Sommer *et al.* 1985, 1987; Wessler *et al.* 1986). Thus, there is clear evidence that insertion and excision of transposons from a gene site generates sequence divergence. Schwarz-Sommer *et al.* (1985) concluded that the insertion and excision of transposons generates functionally active, but structurally altered gene products. Wessler *et al.* (1986) have demonstrated that transposon insertion and excision resulted in altered *Wx* enzymatic activity.

The sequence divergence generated by transposons or receptor elements mobilized by transposons may give rise to potentially new and useful alleles that can be utilized in selection. There is some evidence that transposon-induced variation increased selection response in *Drosophila melanogaster* (Mackay, 1984, 1985). Torkamanzehi *et al.* (1988), in a study similar to Mackay's (1985), however, found no evidence of transposon-induced selection responses in Drosophila. Similar studies in plant species have not been reported. Our study differs from those in Drosophila in that the transposons in the Drosophila experiments were mobilized prior to selection, whereas we examined how the frequency of *Uq* had changed after completion of selection. The data in our study cannot be used to draw conclusions about transposon-induced selection responses, but the presence of *Uq* in the BSSS populations suggests that this element has the potential for generating new genetic variation.

In conclusion, our data suggest that the spread of *Uq* after half-sib and S_2 progeny recurrent selection was predominantly due to random genetic drift coupled with a selective advantage possibly associated with a region of the genome linked to *Uq*. The extinction of *Uq* after reciprocal recurrent selection was best explained by random genetic drift. Experiments are being planned to provide additional information on the population dynamics of *Uq* in BSSS.

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