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B.-S. Seo · P. A. Peterson

A transposable element in diverse corn lines, *Ubiquitous* (*Uq*): allelism test

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Abstract Since the discovery of the *Uq* transposable element system in the early 1980s, studies of *Uq* distribution have shown that *Uq* is pervasive in genetic stocks and corn populations including BSSS, the Illinois oil and protein lines, 'Lancaster', 'Jarvis' and several others. The assumption made was that *Uq* might have provided the variation that has contributed to maize breeding progress. Of the several inbreds tested in previous studies, only Ial159, one of the contributors to BSSS, contained an active *Uq*. The main question posed in our experiments was that of chromosomal location(s), or allelic relationships, of active *Uq* elements in diverse corn populations. Results showed that these *Uq* elements are allelic, linked or independent, though most found from corn populations show quite distant or independent linkage relationships with each other. The lack of a linear linkage map among these *Uq* elements may be interpreted to have resulted from transposition events and this might have led to the differentiated instability of an individual *Uq* element that was found to be variable. Other questions also discussed relate to the origin of *Uq* elements in corn populations and their role(s) in plant breeding.

Key words Maize breeding lines · Transposable element · *Ubiquitous* (*Uq*) · Complex allelism · Role of *Uq* in maize breeding

Introduction

The *Uq-ruq* (*Ubiquitous*) transposable element system was initially characterized in genetic tests conducted by Friedemann and Peterson (1982) in G. F. Sprague's Aberrant Ratio lines, which originated from stocks exposed to BSMV (Barley Striped Mosaic Virus) (Sprague and McKinney 1966, 1971). In studies of the distribution of *Uq* in genetic stocks, several autonomous and nonautonomous elements have been isolated (Friedemann and Peterson 1982; Pereira and Peterson 1985; Caldwell and Peterson 1989; Pan and Peterson 1988b, 1991a, b).

Quiescent *Uq* sequences in maize inbreds are spontaneously activated both somatically and germinally in a random manner (Pan and Peterson 1988b, 1989, 1991a). In one case a *Uq* (*Mn::Uq*) was activated via 5-aza-2′-deoxycytidine treatment, which then cosegregated with the maize *Miniature* locus. The origin of *Mn::Uq* in this manner confirms that *Uq* transposes. The origin *ruq* elements inserted at the *a1* and *c1* loci, respectively, established that nonautonomous *ruq* elements also transpose (Friedemann and Peterson 1982; Caldwell and Peterson 1989).

The diversity of *Uq* elements is illustrated by several of the *Uq* elements from genetic stocks (Pereira and Peterson 1985; Caldwell and Peterson 1989) and those spontaneously activated germinals (Pan and Peterson 1991a) that express distinguishable distinct aleurone spotting patterns through interaction with reporter alleles. The *Mn::Uq* mutant can, for example, transactivate the *a-ruq* allele but not a normal *Uq*-responsive *c-ruq* allele (Pan and Peterson 1989). The different *Uq* transactivation functions can be accounted for by the composition hypothesis (McClintock 1958) or the position hypothesis (Peterson 1977). Genetic diversity among *Uq* elements may not be surprising since most have arisen by spontaneous activation, possibly resulting in partial activation. If this is the case, it is likely that the methylation intensity of *Uq* sequences, especially in the 5′ region, may vary, thereby modifying the promoter strength that controls element activity (Chandler and Walbot 1986; Dennis and Brettell 1990; Bird 1992). De novo methylation is hypothesized to occur gradually and thus takes several generations to complete, whereas demethylation can be rapid due to the failure of maintenance methylation (Otto and Walbot 1990).

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B.-S. Seo · P. A. Peterson (✉)
Agronomy Department, Iowa State University, Ames, IA 50011, USA

In a molecular characterization of the *Uq* system's components, it was found that *ruq* has approximately a 95% homology to *Ds1* and produces the 8-bp target site duplication upon insertion (Pisabarro et al. 1991), indicating that the *Uq-ruq* system is a modified *Ac-Ds* system. The finding that the functions of the *Ac* and *Uq* systems overlap [*Uq* transactivates *Ds1* only while *Ac* or four doses of *Ac2* induce responses from all of the *ruq* elements (Caldwell and Peterson 1992)] provides further support.

Uq distribution studies in diverse corn lines and populations have established that breeding materials contain active mobile elements. Among the known active elements, only *Uq* and *Mrh* are prevalent in small samples of BSSS (Iowa Stiff Stalk Synthetic) populations (Peterson and Friedemann 1983; Peterson and Salamini 1986). Only 1 of the original 16 inbreds (inbred Ial159) used to construct the BSSS population contains *Uq* (Cormack et al. 1988). Possibly, selection against variability and for uniformity and stability during inbred line development resulted in stable lines in which active *Uq* elements were silenced or segregated out (Peterson 1988), signifying a role of the element in maintaining genetic variability of the populations. Perhaps *Uq* elements can become methylated and thereby inactive, as occurs with other transposable elements (Bennetzen 1987; Chomet et al. 1987; Banks and Fedoroff 1989; Dennis and Brettell 1990). The *Mn*::*Uq* induced by a demethylation treatment supports this methylation option.

Lamkey et al. (1991) in a test of BSSS cycle populations found changes in the frequency of *Uq* in two independent, closed recurrent selection programs: 13 cycles of half-sib and S_2 progeny recurrent selection and 11 cycles of reciprocal recurrent selection. With the half-sib and S2 progeny recurrent selection (19–91%) there was an increase in the frequency of active *Uq* elements, which was ascribed to random genetic drift and possibly from the selective advantage of a favorable genome segment linked to *Uq* as an alternative. In the reciprocal recurrent selection program, the frequency of active *Uq* elements gradually decreased and was not found in BSSS(R)C6 and later generations. This extinction of the presence of *Uq* was suggested to result from random genetic drift.

Maize populations such as BSSS (Hallauer et al. 1983) and the Illinois oil and protein lines (Dudley 1976) have considerable genetic variability, and this has been displayed by isozyme (Goodman and Stuber 1983) and restriction length polymorphism (RFLP) analysis (Helentjaris et al. 1985; Sughroue and Rocheford 1994). However, what underlies this variability still remains unanswered. Transposable elements do generate additional sequences upon insertion, thereby increasing the genome size, and upon excision leave footprints leading to altered gene sequences. This mechanism provides genetic diversity (Schwarz-Sommer et al. 1985), but whether this diversity has favorable effects on corn populations is yet to be determined. As an initial step to inquire into the possible roles of transposable elements in corn populations, this study was undertaken to determine the allelic relationships among *Uq* elements discovered in numerous and diverse cornbelt populations and genetic stocks. Is the founder *Uq*(I159) the only *Uq* present in the BSSS population? *Uq* elements vary in position; they are either allelic, linked or independent, and most from corn populations have quite distant or independent linkage relationships, a finding that supports the concept that *Uq*-transposed or quiescent types became activated.

Materials and methods

Source materials

The 23 *Uq* elements examined in this study, 16 alleles from cornbelt populations, 6 from genetic stocks and 1 via spontaneous activation, are listed in Table 1. Several of these corn lines have a relationship or a common origin at some distant past.

The basis for the mapping strategy

This mapping study for the various *Uq* elements is unusual in that no known genetic markers are available, because none have been tagged with any distinguishable marker on a chromosome, with the result that this study is confined to the linkage relationships of each *Uq* to the others. However, mapping is possible by monitoring *c-ruq* events in the presence of an active *Uq*. Table 2 illustrates the rationale and assay supporting this mapping study and includes the determination of the ratio of spotted to colorless kernels on an ear that identifies *Uq* linkage relationships in the presence of homozygous *c-ruq*. Allelic in this context is used to identify very closely linked *Uq* elements, or identical elements at the same chromosome site. It should be noted that because only half of the recombinants can be recovered as colorless kernels (Table 2), the linkage value will be double the percentage of observed recombinants (linkage value=[(number of colorless/number of total) × 100] × 2). No attempt was made, because of the lack of a marker, to map the elements to a specific chromosome marker.

Variables to consider in the mapping of *Uq*'s

Several variables influence the determination of *Uq* linkage relationships, and this is defined as 'instability (I),' expressed as colorless kernels probably resulting from the inactivation or loss of *Uq* sequences. I could also be partly due to changes in the *c-ruq* allele or to the transposition of *Uq*. Further details on these variables will be discussed in the Discussion section.

Crossing strategy

Because most maize populations carry at least one recessive *c1* allele (Peterson 1986; Cormack et al. 1988), *c-ruq* was used as a reporter allele for screening populations for active *Uq* elements. The *c-ruq* allele was used mainly as the male because of the inconsistent segregation of spotted and colorless kernels in the reciprocal crosses between *Uq* and *c-ruq* (Pan and Peterson 1991b).

These experiments were resolved into two parts: (1) control and (2) mapping. The control experiment was designed to estimate the extent of genetic instability of each *Uq*, and the mapping experiment was used to determine the allelic or linkage relationships between 2 *Uq* elements. Thus a 'diallel cross' with all possible combinations was performed among 23 *Uq* elements. Cross 1 describes the general crossing strategy used to construct control homozygotes for each *Uq* (e.g. *Uq-1/Uq-1*). Selected kernels were crossed by *c-ruq* to measure the instability (I) of each *Uq*. Cross 2 develops the heterozygotes for each set of 2 *Uq* elements. Selected kernels were crossed by *c-ruq* for mapping (Cross 3). Kernel selections were made to rescue at least one homozygote (Cross 1 progeny) or one heterozygote

Table 1 Index of terms and lists of *Uq* elements used in this study

Term/*Uq* Entries	Description and References
Uq	An active transposable element that induces mutability of *ruq*-containing alleles
ruq	A defective element in the *Uq-ruq* system, expresses mutability in the presence of *Uq*
Uq-BSSSC5	A BSSS population after five cycles of selection (Hallauer et al. 1983; Peterson and Salamini 1986)
Uq-BS13(S)C4	A BSSS after seven cycles of half-sib and four cycles of S2 recurrent selection (Cormack et al. 1988)
Uq-I159	Ial159, one of the 16 inbreds that were used to develop BSSS (Cormack et al. 1988)
Uq-BSLE(ML)C10	A BSLE (Iowa Long Ear Synthetic) population after ten cycles of long ear selection (Cortez-Mendoza and Hallauer 1979; Cormack et al. 1988)
Uq-BSLE(MS)C15	A BSLE after 15 cycles of short ear selection (Cormack et al. 1988)
Uq-RHP1968	One of the Illinois oil and protein lines, RHP (Reverse High Protein) after 21 cycles of high protein selection (Dudley 1976; Cormack et al. 1988)
Uq-SHO1968	One of the Illinois oil and protein lines, SHO (Switchback High Oil) after 14 cycles of high oil selection (Cormack et al. 1988)
Uq-HGC25	A Hays Golden population after 25 cycles of mass selection (Gardner 1976; Cormack et al. 1988), later confirmed as *Ac* in our lab (Peterson unpublished)
Uq-Hiloss	Hi-loss B's population (Rhoades and Dempsey 1982, 1983; Pan and Peterson 1988a)
Uq-Jarvis	Jarvis Golden Prolific (Moll et al. 1977)
Uq-LC	Lancaster (Walejko & Russell 1977; Cormack et al. 1988)
Uq LS	Lancaster Surecrop (PI280061) (Smith 1986; Cormack et al. 1988)
Uq-RYD	Reid's Yellow Dent (PI213698) (Smith 1986; Cormack et al. 1988)
Uq-PDent	Polar Dent (PI222474) (Smith 1986; Cormack et al. 1988)
Uq-EC	Echelberger Clarage (PI278713) (Smith 1986; Cormack et al. 1988)
Uq-SK	Silver King (PI280853) (Smith 1986; Cormack et al. 1988)
Uq-St	First isolated standard *Uq* element (Friedemann and Peterson 1982), *Uq1* (Pan and Peterson 1991a)
Uq-13	Isolated from the *Uq*-controlled *a-m13* mutant, distinguishes *a-ruq* from *c-ruq* in terms of their spotting patterns (Pereira and Peterson 1985; Caldwell and Peterson 1989)
Uq-16	Isolated from the *Uq*-controlled *a-m16* mutant, displays a lower spotting pattern than *Uq-St* (Pereira and Peterson 1985)
Uq-31, *Uq-66* and *Uq-67*	Isolated from stocks carrying *Uq-St* (Caldwell and Peterson 1989)
Uq-870621Y	Germinal isolate originating from spontaneous activation, *Uq2* (Pan and Peterson 1991a)

Table 2 Expected frequency of spotted kernels in the various element arrangements in the presence of *c-ruq/c-ruq*

Two *Uq*'s	Arrangements	Spotted kernels (%)
Allelic	*Uq-1* / *Uq-2*	100
Independent	*Uq-1* / + ; + / *Uq-2*	75
Linked	*Uq-1* + / + *Uq-2*	75 < sp < 100[a]
One *Uq*	*Uq-1* + / + +	50

[a] Gamete genotypes from two linked *Uq* elements are *Uq-1* +, + *Uq-2*, *Uq-1 Uq-2* and + +. Spots induced by noncrossovers, *Uq-1* and *Uq-2*, are not distinguishable from spots by the crossover *Uq-1 Uq-2*. Only half the recombinants are detectable as colorless kernels without *Uq* (+ +). Thus, the linkage value calculation method will be [(number of colorless/number of total) × 100] × 2

(Cross 2 progeny) at the 95–99% level. However, the selections were not random because the kernels showing a heavier spotting pattern were generally favored to insure that 2 elements were present, that is to say we took advantage of positive dosage effects.

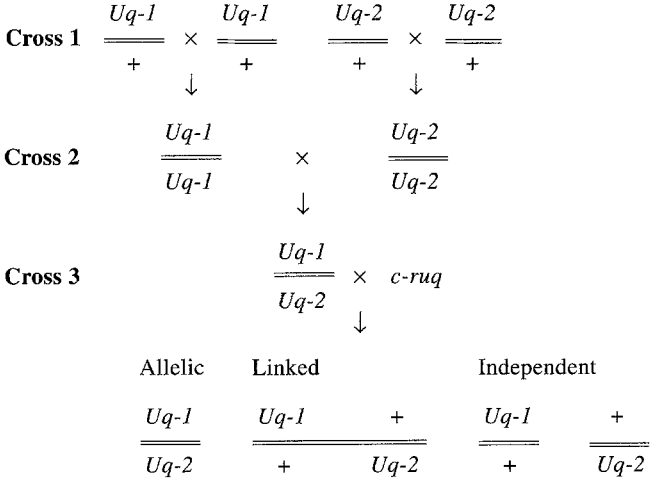

Table 3 An example illustrating the data selection procedure from control experiments (*sp* spotted, *cl* colorless)

Uq-RHP1968: Original data (χ^2-test: $\alpha = 0.05$, Value = 3.84)

Xn[a]	sp	cl	Total	% sp	3 sp:1 cl (χ^2-test)	1 sp:1 cl (χ^2-test)
X1	203	0	203	100.00	67.66**	
X2	209	3	212	98.58	62.88**	
X3	198	3	201	98.51	59.22**	
X4	96	2	98	97.96	27.54**	
X5	69	46	115	60.00	13.80**	4.58*
X6	108	83	191	56.54		3.26
X7	132	110	242	54.55		2.00
X8	63	57	120	52.50		0.30
X9	97	97	194	50.00 (= 100.00)[b]		0.00
X10	61	64	125	48.80 (= 97.60)		0.06
X11	55	59	114	48.25 (= 96.50)		0.14
X12	74	110	184	40.22		7.04**
X13	63	96	159	39.62		6.84**

* Significant, ** Highly significant,
[a] Serial number of harvested and counted ears,
[b] Doubled% sp to make homozygous for instability calculation

Control experiments: data selection and instability calculation

Controls were developed to estimate the instability of individual *Uq* elements. Thus, data to be selected for this purpose must indicate that all four copies of the element after replication were transmitted to the progeny. That is, kernels without spots were assumed to come from instability. Without instability, homozygous plants would be expected to produce 100% spotted kernels (spots) on an ear, and hemizygous plants would give 50% spots.

An example of data selection and instability calculation is demonstrated with the controls of *Uq-RHP1968* in Table 3. The following assumption was made for data selection: 75% spots on an ear would result when 1 element was inactivated or lost after replication. Under this criterion, crosses having more than 75% spots were selected that failed the chi-square test of 3 spotted:1 colorless. In the case of hemizygosity, which was used to complement the lack of data, errors due to random transmission can produce values with somewhat more or less than 50% spots. Data with more than 50% spots were excluded because the purpose was to measure the extent of instability. Data were included that passed the chi-square test of 1 spotted:1 colorless and subsequently doubled for a homozygous value. As explained, X1-X4 were selected, and X9-X11 were selected, and each doubled for the homozygous value (Table 3). From the selected data, the average percentage of spots was found to be 98.45±0.48. Thus, the instability of homozygosity or two copies of *Uq-RHP1968* would be 1.55 (=100–98.45)±0.48. Therefore, the instability of one copy will be (1.55±0.48)/2=0.77±0.24.

Mapping experiments: data selection and linkage calculation

In the mapping experiments, the purpose was to determine whether two independently isolated or originating *Uq* elements were allelic, linked or independent of each other. Experimental results have shown that data are quite variable, ranging from approximately 15% to 100% spots (data not shown, Seo 1994). The outcome of this wide range of values is discussed in the Discussion section. Data required for this study should represent at least approximately 75% spots or more, the case for independent or linked relationship (Table 2). Data with approximately 50% spots that passed the 1:1 chi-square test were first precluded. This test supports the idea that there was originally only 1 element present, and this datum was no longer considered.

With respect to instability, the selection procedure among the data of mid-values between more than 50% spots and less than 75% spots that failed both the 1:1 and 3:1 chi-square tests was rather complex. Once the data failed the 1:1 test, it was assumed that their parents originally had 2 elements. For the same reason, even if the data failed the 3:1 test, it was not considered that their parents originally contained 1 element. In the control experiments a maximum of approximately 10% instability was observed (Seo 1994). Whether these mid-values would be selected depended on the 3:1 chi-square test and the size of the estimated instability of a pair of 2 *Uq* elements, that is, the lowest value that was temporarily determined for data selection under the assumption of independence.

An example of the lowest value calculation is illustrated with the pair *Uq-BSSSC5* and *Uq-I159*. Their instabilities are 0.81±0.80 and 3.84±1.14, respectively. Therefore, the theoretical instability of the heterozygotes containing these 2 *Uq* elements will be (0.81±0.80)+(3.84±1.14)=4.65±1.94. Two standard errors are mathematically added because the 2 *Uq* elements are each segregating in different kernels; only one-fourth of the kernels on an ear would carry the 2 together. Given that *Uq-BSSSC5* and *Uq-I159* are independent, 75% spots will be produced. Because of instability, however, the independent value of these 2 particular *Uq* elements can be corrected as 75–(4.65±1.94)=70.35±1.94. Therefore, the lowest value to be selected would be 68.41 (=70.35–1.94). Data selection procedures for the mapping experiments are illustrated with a set of progeny data from *Uq-BSSSC5* versus *Uq-I159* in Table 4. As explained previously, values of 68.41 or more, those that are non-significant in the 3:1 test, or those larger than 75%, will be selected. Therefore, X1–X5 are selected from Table 4, and with these selected data Table 5 illustrates the steps to linkage calculation.

Because of instability, it is difficult to conclude that outliers in linkage values among sister lines are derived from transposition, inactivation or loss. The confirmation of transposition was not made, although a clear deviant, for example from allelic or close linkage to independence, can easily be detected in the next generation. Modifications of linkage calculation were tried; apparent outliers that failed the chi-square homogeneity test were regarded as resulting from transposition events and not included in the linkage calculation. Another major problem is that it is not possible to determine an expectation on the ratio of spotted to colorless since the linkage values of any set of 2 *Uq* elements are not known. This problem can be resolved by the chi-square test in the R↔C table (Snedecor and Cochran 1967). The formula for the chi-square test is as follows:

$\chi^2 = \Sigma\,[(f-F)^2/F]$
f = observed value,
F = expected value = (row total) (column total)/total
$df = (R-1)(C-1)$

With this formula, the chi-square test was performed as shown in Table 5.

Table 4 An example illustrating the data selection procedure from mapping experiments (*sp* spotted, *cl* colorless)

Uq-RHP1968: Original data (Lowest value = 68.41, χ^2-test: $\alpha = 0.05$, Value = 3.84)

Xn[a]	sp	cl	Total	% sp	3 sp:1 cl (χ^2-test)	1 sp:1 cl (χ^2-test)
X1	361	39	400	90.25	49.60**	
X2	133	31	164	81.10	3.24	
X3	106	32	138	76.81	0.24	
X4	232	79	311	74.60	0.02	
X5	387	146	533	72.61	1.61	
X6	269	126	395	68.10	10.01**	
X7	139	78	217	64.06	13.85**	
X8	89	56	145	61.38	14.34**	7.50**
X9	207	145	352	58.81		10.95**
X10	64	52	116	55.17		1.24

** Highly significant,
[a] Serial number of harvested and counted ears

Table 5 *Uq-BSSSC5* versus *Uq-I159*: Selected data and procedures for linkage calculation (*sp* spotted, *cl* colorless)

χ^2-test: $\alpha = 0.05$, d.f. = 4, Value = 9.488

Xn[a]	sp	cl	Total	% sp	χ^2-test
X1	361	39	400	90.25	31.177
X2	133	31	164	81.10	0.497
X3	106	32	138	76.81	0.344
X4	232	79	311	74.60	3.369
X5	387	146	533	21.61	12.447
Total	1219	327	1546		47.834

Since 47.834 > 9.488, X1 that shows the largest Chi-square value was excluded and the Chi-square test was made again as follows:

χ^2-test: $\alpha = 0.05$, d.f. = 3, Value = 7.815

Xn1	sp2	cl3	Total	% sp	χ^2-test
X2	133	31	146	81.10	3.382
X3	106	32	138	76.81	0.277
X4	232	79	311	74.60	0.012
X5	387	146	533	72.61	1.448
Total	858	288	1146		5.119

The average of spotted kernels is 74.87% [= (858/1146) × 100]
The percentage of recombinants (cl) is 25.13 (= 100–74.87)

[a] Serial number of harvested and counted ears

As shown in Table 5, the average percentage of spots is 74.87 [=(858/1146) × 100], and the standard error 1.99. Therefore, the percentage of recombinants (cl) is 25.13 (=100–74.87)±1.99, and the linkage value between *Uq-BSSSC5* and *Uq-I159* would be approximately 50.26 (=25.13 × 2), which indicates independence. This linkage value, however, includes instability of the 2 elements because the selected data are assumed to include instability, which is 4.65±1.94, as explained. Therefore, the average percentage spots should be corrected as (74.87+4.65)±(1.99+1.94)/2=79.52±1.97. Theoretically, two standard errors are expected to be the same (i.e. 1.99=1.94), since they were derived from a composite of *Uq-BSSSC5* and *Uq-I159*. Their standard error was therefore corrected by averaging out two values. So, the percentage of recombinants is 100–(79.52±1.97)=20.48±1.97 and the estimated linkage value is 40.96 (=20.48 × 2), indicating that *Uq-BSSSC5* and *Uq-I159* are linked to each other.

Results

Instability from control experiments

The instability of one copy of each *Uq* ranged from 0.42 for *Uq-Jarvis* (the lowest value) to 4.59 for *Uq-BS13(S)C4* (the highest value) (Seo 1994). With 10% instability, the independent segregation of 75% spots was reduced to approximately 65% spots as, for example, in the experimental data of *Uq-BS13(S)C4* versus *Uq-LC* (data not shown, Seo 1994). The average instability of all *Uq* elements was approximately 2%, indicating that the *Uq* function can be expected to be lost in 2 out of 100 individual copies in hemizygotes or 4 out of 100 in homozygotes.

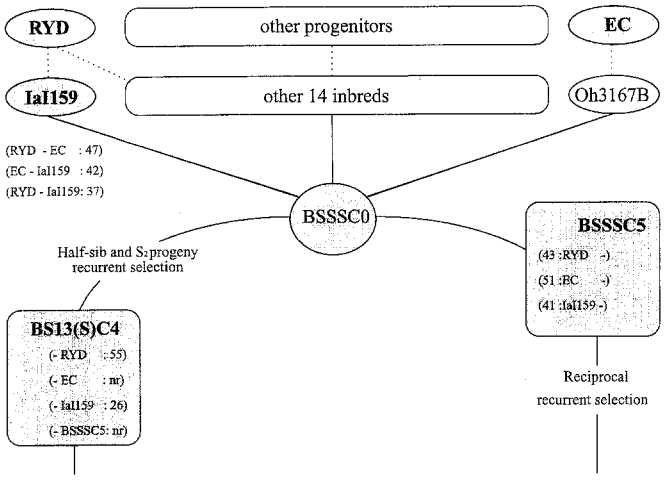

Fig. 1 Outlined pedigree of BSSS and linkage relationships among *Uq* elements discovered from the BSSS-related inbreds and populations. The *first line* indicates the direct or indirect progenitors of the 16 inbreds in the *second line*, which were used for the synthesis of BSSS (for details on pedigree, see Hallauer et al. 1983; Lamkey et al. 1991). Populations or lines in the *shaded areas* carry active *Uq* elements. Linkage values between 2 *Uq* elements are indicated in *brackets*. This illustration suggests it is possible that the 2 *Uq* elements in BSSSC0 (Lamkey et al. 1991) came from RYD and EC, respectively. The linkage relationships among the BSSS-related *Uq* elements are a typical example of those found among *Uq* elements uncovered from corn breeding populations (*RYD* 'Rield Yellow Dent', *EC* 'Echelberger Charge',*nr* not rescued)

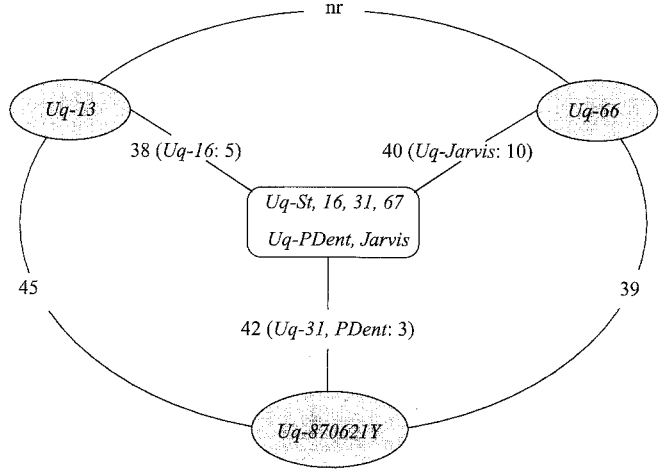

Fig. 2 Linkage relationships among *Uq* elements discovered from genetic materials, plus two corn populations, 'Polar Dent' and 'Jarvis'. *Numbers* represent linkage values between connected *Uq* elements: the 6 (*Uq-St, 16, 31, 67, Pdent* and *Jarvis*) in the *center* are allelic; the 3 (*Uq-13, 66* and *870621Y*) in the *shaded ovals* seem to be far-linked to the allelic *Uq* elements in the center as interpreted from the large linkage values and some exceptions indicated in the *parenthesis*. Small linkage values in the parenthesis might have resulted from the sampling of transposition events (*nr* not rescued)

Linkage values from mapping experiments

The linkage values of different *Uq* elements revealed that a linear linkage map could not be drawn. Linkage relationships showed a large distance or almost independence especially among the *Uq* elements from breeding lines and populations. Among genetic materials and some breeding sources the *Uq* elements seemed to be located on one chromosome. On the basis of this observation, there seemed to be two groups. The first group includes *Uq* elements from breeding sources that predominantly have large linkage values. A typical example is illustrated with BSSS-related *Uq*'s in Fig. 1. The second group includes *Uq* elements from genetic materials that appear to be clustered on one chromosome; these intermingled relationships are shown in Fig. 2. Linkage values between the first and second groups were also similar to those in the first group. Because these results indicated that *Uq* elements seem to be distributed over the genome, the drawing up of linear maps does not appear to be useful. So rather than attempting linear linkage maps as in most linkage studies, an investigation of the results coupled with the pedigree analysis of some *Uq* sources was undertaken and is considered in the next section.

Comparison of expected linkage relationship from the pedigree analysis of *Uq* sources with the allelic tests

Uq elements related to corn breeding lines or populations

The possible linkage relationships among some *Uq* elements can be anticipated on the basis of results from previous studies and by tracing the pedigrees of corn lines and populations from which the *Uq* elements were uncovered.

BSSS-related. The BSSS population was developed by Sprague (1946) by intermating 16 inbred lines in 1933 and 1934. Hallauer et al. (1983) suggested that most of the lines, including IaI159, were derived from sources that included 'Reid's Yellow Dent' germplasm and an 'Echelberger Clarage' line, Oh3167B. IaI159, BSSSC5, BS13(S)C4 and 'Echelberger Clarage' (PI278713) carry active *Uq* elements (Cormack et al. 1988). In the limited sampling of Oh3167B (three ears), *Uq* was not detected. It is possible that other inbred lines derived from one of the 'Reid's Yellow Dent' strains might also contain *Uq* since 'Reid's Yellow Dent' (PI213698) was found to have an active *Uq*. It is therefore probable that 2 *Uq* elements, 1 from IaI159 and the other from 'Echelberger Clarage' or one of the inbreds from 'Reid's Yellow Dent' background, were introduced into BSSS. This presumption supports the observed frequency of *Uq* (0.10) in BSSSC0 (Lamkey et al. 1991). Unexpectedly BSSS-related *Uq* elements [*Uq-RYD, Uq-EC, Uq-I159, Uq-BSSSC5* and *Uq-BS13(S)C4*] revealed large linkage distances and in most cases independence as illustrated by the probable BSSS pedigree in Fig. 1. Both lines of descent (Fig. 1) following the formation of BSSSC0 represent two different selection programs. The relationships among these *Uq* elements represent those among the first group.

Lancaster Surecrop-related. The BSLE population was synthesized by combining 12 inbred lines (Russell et al.

1971a,b). Mass selection for divergent short and long ear length was initiated in the 1963 isolation planting with a selection intensity of 7.5% (Cortez-Mendoza and Hallauer 1979). One of the inbreds, C103, and 'Lancaster' were derived from 'Lancaster Surecrop' (Gerdes and Tracy 1993). Another inbred, (Lanc. × Comp.)-34, might also contain *Uq* delivered from 'Lancaster'. A close relationship might be expected among *Uq* elements from 'Lancaster Surecrop' (LS), 'Lancaster' (LC), BSLE(ML)C10 and BSLE(MS)C15, however as linkage distances were between 32.84 and 43.66, a linear relationship does not exist.

Isozyme analysis-related. 'Lancaster Surecrop', 'Reid's Yellow Dent', 'Polar Dent', 'Echelberger Clarage' and 'Silver King' are open-pollinated cultivars (Smith 1986). Smith (1986) investigated genetic diversity among open-pollinated varieties of the corn belt dent racial complex of maize using 21 isozyme loci. Principal component analysis of the isozyme allele frequencies revealed that 'Lancaster Surecrop' pedigrees were separated from 'Reid's Yellow Dent', and that pedigrees of 'Polar Dent', 'Echelberger Clarage' and 'Silver King' might be associated with one another. This interpretation suggests that *Uq-PDent*, *Uq-EC* and *Uq-SK* could be correlated, however, in most cases, relationships among these *Uq*'s disclose that the linkage intervals are more than 35.

Illinois oil and protein line-related. Selection of the Illinois oil and protein lines was initiated in 1896 by analyzing 163 open-pollinated ears of the 'Burr's White' variety for percent oil and percent protein (Dudley 1976). *Uq* content was identified in RHP1968 (RHPC21) and SHO1968 (SHOC14) (Cormack et al. 1988) suggesting the same *Uq*, but the linkage between the 2 is 44.68.

Any relation of Jarvis Golden Prolific and Hays Golden to other corn lines or populations previously discussed is not known. The linkage value between *Uq-Jarvis* and *Uq-HGC25* was 1.92 (possibly allelic), however they were not allelic to other *Uq* elements according to this study. But the linkage relationships on the basis of the pedigree analysis of each of these 2 *Uq* elements to others were somewhat variable.

These data related to corn breeding lines strongly support the concept that *Uq* is not a unique Mendelian locus but has transposed in the past over the host chromosomes, or alternatively that quiescent *Uq* elements have been independently activated at various positions in the genome.

Uq elements derived from genetic stocks

It has been suggested that *Uq-St* is located on chromosome 2. *Uq-St* is allelic to *Uq* (*a-et* line), which is linked to a chromosome 2–9b *wx* translocation (cM is not known), and it appears to be independent of, but may be far-linked to, *Uq-13* (≈45 cM) (Pereira and Peterson 1985). Under the assumption that different positions could be responsible for distinct spotting patterns induced by different *Uq* elements, spotting patterns induced by *Uq-St*, *Uq-13* and *Uq-16* (Pereira and Peterson 1985; Caldwell and Peterson 1989) may provide a clue that they are not allelic. Each *Uq* was discovered independently with separate pedigrees from stocks 5–12 generations after BSMV treatment.

Uq-31 was isolated as a spotted round kernel from the 1979 isolation plot. *Uq-66* and *Uq-67* arose on the same ear from the 1980 plot from stocks that carried *Uq-St* in pedigree and were phenotypically identical with *Uq-St*, suggesting that they could be re-isolates of *Uq-St* (Caldwell and Peterson 1989). *Uq-870621Y* is a germinal isolate (Pan and Peterson 1991a) and known to be independent of *Uq-St* (Pan and Peterson 1991b).

The *Uq* linkage values from genetic stocks, plus *Uq-PDent* and *Uq-Jarvis* from breeding populations, are presented in Fig. 2. The results of this study illustrate that the 6 *Uq* elements found in the center of the plot in Fig. 2 (*Uq-St*, *Uq-16*, *Uq-31*, *Uq-67*, *Uq-PDent* and *Uq-Jarvis*) are allelic or reside in a very small linkage block, whereas the other 3 *Uq* elments (*Uq-13*, *Uq-66* and *Uq-870621Y*) seem to be somewhat independent of the 6 allelic ones and far-linked from each other. There are, however, three groupings that show a clear linkage: *Uq-13* – *Uq-16* (≈5 cM), *Uq-66* – *Uq-Jarvis* (≈10 cM), and *Uq-31* and *PDent* – *Uq-870621Y* (≈3 cM). These small linkage values might be a result of transposition events. This result supports the contention stated in the previous studies that *Uq-13* and *Uq-870621Y* are independent of *Uq-St*. Our study also demonstrated that *Uq-13* and *Uq-870621Y* seem to be independent of each other (≈45 cM).

The clear allelism of *Uq-St* and *Uq-16* refutes the past presumption based on dissimilar spotting patterns that they might be located at different sites (Pereira and Peterson 1985). In a molecular analysis, *a1-ruq* and *a1-m16* were shown to be the same allele; they contain the first 100 bp that are identical and are inserted at the same position and in the same orientation (Pisabarro et al. 1991). Thus, there must be some functional differences between *Uq-St* and *Uq-16*.

Uq-St, *Uq-31*, *Uq-66* and *Uq-67* are either allelic, closely linked or almost independent, but none that are clearly independent are on chromosome 2 (Pereira and Peterson 1985). This was supported by the allelic test determination that showed that these *Uq* elements are all linked to *Uq-HGC25* (=*Ac*; Peterson, unpublished), although the values are somewhat inconsistent (data not shown, Seo 1994). *Uq-Hiloss* and *Uq-RHP1968* show a close linkage value (≈6 cM), and each has allelic or linkage relationships to those *Uq* elements on chromosome 2 (data not shown, Seo 1994), providing concrete evidence that many are on chromosome 2.

Discussion

Explanation of variable values

The data on percentage of spotted kernels among the allelic test crosses showed a very wide range of values that

varied from 15% to 100% in an extreme case. Discarded values require a reasonable explanation. As stated when we were justifying instability in the Materials and methods section, the unexpected wide range of values can be explained by the instability of (methylation, loss or inactivation) of *Uq*, or partly by *c-ruq*. A simple theoretical mechanism to explain this whole range of quantitative values can be demonstrated that is in accordance with the number of allelic *Uq* elements in each sample before and after replication. First, homozygosity without loss will give 100% spotted kernels (spots). Second, homozygosity with loss or inactivation of one copy after replication will give 75% spots. Third, hemizygosity or heterozygosity due to the loss of one copy before replication will give 50% spots. Fourth, hemizygosity with loss of one copy after replication will give 25% spots.

In addition, quantitative values not included in the linkage calculation may be affected by the partial inactivation of *Uq* elements in individual kernels, combined with the loss or absence of *c-ruq*. Random sampling or transmission error may partly explain values that are slightly deviant from each class (75%, 50% and 25%). Counting errors could be involved because some spots may escape detection. Also, the degree of linkage distance between 2 *Uq* elements is responsible for the varied percentages of spots. If allelic, the loss of one copy after replication will produce 75% spots. If independent, free recombination between them will give 62.5% spots. Therefore, 2 linked *Uq* elements will give a frequency of spots between 62.5% and 75%. Transposition events also, although not frequently, generate variable values. When 2 *Uq* elements are linked, transposition alters the linkage value, and thus the proportion of spotted kernels. If replicative transpositions similar to *Ac* (Chen et al. 1992) would also occur and 2 or more *Uq* copies were present in one strand in a selected kernel, its progeny would not show consistent values.

It was not investigated how often there is a loss or inactivation of *Uq*. However, values far below 25% do not often occur. The mid-values from 25% to 50% vary, but in most cases data close to 50% are predominant, which leads to the conclusion that loss or complete inactivation of a *Uq* sequence before transmission to the progeny is rare. It could therefore be concluded that partial inactivation of individual *Uq* copies, coupled with variable degrees of linkage distance between two *Uq*'s, is mainly responsible for the wide range of mid-values.

Extrapolation on the origin of *Uq* elements

The large linkage values among *Uq* elements definitely suggest that they have transposed over the genome. Some, especially from genetic stocks, are clustered on chromosome 2, and most of the ones from breeding populations have large linkage values or almost independent relationships. The clustering and the wide distribution of *Uq* elements over the genome can be explained in two ways. One, originally there was 1 *Uq* present. The lack of variegated kernels does not indicate the absence of active transposable elements but rather the lack of reporters. Replication and transposition via intra- or interchromosome spread (Dover et al. 1982) of this *Uq* could have resulted in some *Uq* elements becoming clustered around a target site (Founder site) and subsequently dispersed around this site, and others becoming distributed over the genome. The other explanation on the clustering of *Uq*'s is that a number of dispersed quiescent *Uq* sequences, whose distribution could be explained by intra- or interchromosome spread, are present. These sequences can be activated spontaneously or by internal or external stresses (McClintock 1978, 1984; Pan and Peterson 1988b, 1989, 1991a). Clustering can result from the activation of clustered quiescent sequences or from the transposition of activated *Uq* elements to sites adjacent to other sequences.

Several studies with other transposable elements have supported the activation of inactive transposable element sequences and the presence of inactive transposable element copies. Environmental genomic stress or shock factors have been known to stimulate the activation of maize transposable elements (McClintock 1984). These factors include chromosome breakage (Doerschug 1973; McClintock 1978), tissue culture (Peschke et al. 1987), mutagens (Walbot 1986), viral infection (Peterson 1985; Sprague 1986), A-bomb tests (Peterson 1953) and demethylation (for review, Otto and Walbot 1990).

The clustered occurrence of other transposons has also been reported. Nonrandom chromosomal distribution of *Ac*-like sequences on chromosome 4 in four maize inbreds was determined using the recombinant-inbred mapping technique (Johns et al. 1990). Using DNA gel blot hybridization and chi-square tests for independence, Ingels et al. (1992) found that 34 of the progeny of a cross between a *Mutator* plant and a non-*Mutator* plant carried *Mu* elements occurring in clusters in the maize genome.

Possible roles of *Uq* in corn breeding progress

Our results show that several *Uq*'s are allelic, linked or independent. More interestingly, most of the *Uq* elements found from corn populations show quite distant or independent linkage relationships. Those from genetic sources appear to be clustered on one chromosome. Lack of a linear linkage map among these *Uq* elements can result from *Uq* transposition events. As previously discussed, either *Uq* has had a single origin and has moved or *Uq* elements have arisen spontaneously. If *Uq* has transposed around the genome, genetic diversity was created by virtue of the characteristics of transposon movements. *Uq* might have survived small breeding selection intensities in corn breeding by creating favorable alleles and shutting down negative genes, resulting in favorable epistasis. It can not be excluded that *Uq* changes in distribution have been altered via genetic drift (Lamkey et al. 1991).

The generation of new alleles has been motivated by a mechanism inducing genetic diversity and can reasonably support the maintenance of genetic variance in breeding populations. Recombination is one mechanism responsible

for the generation of genetic variance. For the past couple of decades, there has been clear evidence that transposable elements have created new mutant alleles by mediating genetic instability, generating stable null mutants and modifying enzymatic properties and genetic suppression (for review, Wessler 1988; Gierl et al. 1989). It is not unusual that both the insertion and excision of transposable elements induce functionally active but quantitatively and qualitatively altered gene products, resulting in new alleles. These phenomena have been available genetically and molecularly, especially in genes involved in the anthocyanin pathway and two of the most-studied maize genes, *Wx* and *Adh1* (McClintock 1951; Echt and Schwartz 1981; Schwarz-Sommer et al. 1985; Wessler et al. 1986; Schiefelbein et al. 1988; Peterson 1990; Dawe et al. 1993). Such a saga of mobile elements may be a mechanism to generate favorable alleles or those useful for the expression of breeding selection standards.

Transposon-induced mutations can control gene expression positively and negatively. *Waxy* proteins from *wx* mutant alleles with and without *Ds* were shown to produce a range of enzymatic activities (Schwarz-Sommer et al. 1985; Wessler et al. 1986). *Adh1-Fm335* (*Ds1* at position+53 in the untranslated leader) reduced steady state mRNA to 1% of wild-type levels (Dennis et al. 1988). RNA protection assays of revertants of the *Ds1*-induced mutation *Adh1-Fm335* (Dawe et al. 1993) illustrated a naturally occurring over- and under-expression of mutants ranging from 48% to 163% of the wild-type *Adh1* level in maize pollen resulting from changes in steady state levels of mRNA. Biochemical and molecular studies of *Bz-McC* (wild-type), *Bz-wm* (*Ds1* upstream of the transcription start site) and its revertants confirmed that three additional nucleotides are accountable for the altered thermal stability of the enzyme and that *Ds1* influences the steady-state level of *Bz*-specific protein and RNA (Schiefelbein et al. 1988).

The role(s) of *Uq* in corn populations remains to be resolved.

References

Banks JA, Fedoroff N (1989) Patterns of developmental and heritable change in methylation of the *Suppressor-mutator* transposable element. Dev Genet 10:425–437

Bennetzen JL (1987) Covalent DNA modification and the regulation of *Mutator* element transposition in maize. Mol Gen Genet 208:45–51

Bird A (1992) The essentials of DNA methylation. Cell 70: 5–8

Caldwell EEO, Peterson PA (1989) Diversity of transposable-element interactions: the *Uq* transposable-element system in maize controls four *c-m* mutants exhibiting unique responses to *Uq-13*. Maydica 34:89–105

Caldwell EEO, Peterson PA (1992) The *Ac* and *Uq* transposable element systems in maize: interactions among components. Genetics 131:723–731

Chandler VL, Walbot V (1986) DNA modification of a maize transposable element correlates with loss of activity. Proc Natl Acad Sci USA 83:1767–1771

Chen J, Greenblatt IM, Dellaporta SL (1992) Molecular analysis of *Ac* transposition and DNA replication. Genetics 130: 665–676

Chomet PC, Wessler S, Dellaporta SL (1987) Inactivation of the maize transposable element *Activator (Ac)* is associated with its DNA modification. EMBO J 6:295–302

Cormack JB, Cox DF, Peterson PA (1988) Presence of the transposable element *Uq* in maize breeding material. Crop Sci 28:941–944

Cortez-Mendoza H, Hallauer AR (1979) Divergent mass selection for ear length in maize. Crop Sci 19:175–178

Dawe RK, Lachmansingh AR, Freeling M (1993) Transposon mediated mutations in the untranslated leader of maize *ADH1* that increase and decrease pollen-specific gene expression. Plant Cell 5:311–319

Dennis ES, Brettell RIS (1990) DNA methylation of maize transposable elements is correlated with activity. Philos Trans R Soc London Ser B 326:217–229

Dennis ES, Sachs MM, Gerlach WL, Beach L, Peacock WJ (1988) The *Ds1* transposable element acts as an intron in the mutant allele *Adh1-Fm335* and is spliced from the message. Nucleic Acids Res 16:3815–3828

Doerschug EB (1973) Studies of Dotted, a regulatory element in maize. I. Induction of Dotted by chromatid breaks. II. Phase variation of Dotted. Theor Appl Genet 43:182–189

Dover G, Brown S, Coen E, Dallas J, Strachan T, Trick M (1982) The dynamics of genome evolution and species differentiation. In: Dover GA, Flavell RB (eds) Genome evolution. Academic Press, New York, pp 343–372

Dudley JW (1976) 76 generations of selection for oil and protein percentage in maize. In: Pollak E, Kempthorne O, Bailey T Jr (eds) Proc Int Cong Quant Genet. Iowa State Univ Press, Ames, Iowa, pp 459–473

Echt CS, Schwartz D (1981) Evidence for the inclusion of controlling elements within the structural gene at the *waxy* locus in maize. Genetics 99:275–284

Friedemann P, Peterson PA (1982) The *Uq* controlling element system in maize. Mol Gen Genet 187:19–29

Gardner CO (1976) Quantitative genetic studies and population improvement in maize and sorghum. In: Pollak E, Kempthorne O, Bailey Jr. T (eds) Proc Int Cong Quant Genet. Iowa State Univ Press, Ames, Iowa, pp 475–489

Gerdes JT, Tracy WM (1993) Pedigree diversity within the Lancaster Surecrop heterotic group of maize. Crop Sci 33: 334–337

Gierl A, Saedler H, Peterson PA (1989) Maize transposable elements. Annu Rev Genet 23:71–85

Goodman MM, Stuber CW (1983) Races of maize VI. Isozyme variation among races of maize in Bolivia. Maydica 28: 169–187

Hallauer AR, Russel WA, Smith OS (1983) Quantitative analysis of Iowa Stiff Stalk Synthetic. Stadler Symp 15:83–104

Helentjaris T, King G, Slocum M, Siedenstrang C, Wegmar S (1985) Restriction fragment polymorphisms as probes for plant diversity and their development as tools for applied plant breeding. Plant Mol Biol 5:109–118

Ingels SC, Bennetzen JL, Hulbert SH, Ellingboe AH (1992) *Mutator* transposable elements that occur in clusters in the maize genome. J Heredity 83:114–118

Johns MA, Fuerstenberg SI, Hennelly CA (1990) Nonrandom chromosomal distribution of *Ac*-like sequences in inbred maize. Genet Res, Camb 55:71–80

Lamkey KR, Peterson PA, Hallauer AR (1991) Frequency of the transposable element *Uq* in Iowa stiff stalk synthetic maize populations. Genet Res 57:1–9

McClintock B (1951) Mutable loci in maize. Carnegie Inst Washington Yearb 50:174–181

McClintock B (1958) The suppressor-mutator system of control of gene action in maize. Carnegie Inst Washington Yearb 57:415–429

McClintock B (1978) Mechanisms that rapidly reorganize the genome. Stadler Symp 10:25–48

McClintock B (1984) The significance of responses of the genome to challenge. Science 226:792–801

Moll RH, Bari A, Stuber CW (1977) Frequency distribution of maize yield before and after reciprocal recurrent selection. Crop Sci 17:794–796

Otto SP, Walbot V (1990) DNA methylation in eukaryotes: kinetics of demethylation and *de novo* methylation during the life cycle. Genetics 124:429–437

Pan Y-B, Peterson PA (1988a) Test for presence of transposable elements in populations. Maize Genet Coop Newsl 62:4–5

Pan Y-B, Peterson PA (1988b) Spontaneous activation of quiescent *Uq* transposable elements during endosperm development in *Zea mays*. Genetics 119:457–464

Pan Y-B, Peterson PA (1989) Tagging of a maize gene involved in kernel development by an activated *Uq* transposable element. Mol Gen Genet 219:324–327

Pan Y-B, Peterson PA (1991a) Spontaneous germinal activation of quiescent *Uq* transposable elements in *Zea mays* L. Genetics 128:823–830

Pan Y-B, Peterson PA (1991b) Newly activated germinal *Uq* elements in maize are clustered on one linkage group independently of the standard *Uq*element. Mol Gen Genet 229:161–174

Pereira A, Peterson PA (1985) Origin and diversity of mutants controlled by the *Uq* transposable element system in maize. Genet Res 46:219–236

Peschke VM, Phillips RL, Gengenbach BG (1987) Discovery of transposable element activity among progeny of tissue culture-derived maize plants. Science 238:804–807

Peterson PA (1953) A mutable pale green locus in maize. Genetics 38:682–683

Peterson PA (1977) The position hypothesis for controlling elements in maize. Mol Gen Genet 149:5–21

Peterson PA (1985) Virus-induced mutations in maize: on the nature of stress-induction of unstable loci. Genet Res 46:207–217

Peterson PA (1986) Mobile elements in maize: a force in evolutionary and plant breeding processes. Proc Stadler Genet Symp 17:47–78

Peterson PA (1988) Transposons in maize and their role in corn breeding progress. In: Loden HD, Wilkinson D (eds) Proc 43rd Annu Corn Sorghum Res Conf. American Seed Trade Assoc, Washington, D.C., pp 51–71

Peterson PA, Friedemann PD (1983) The *Ubiquitous* controlling-element system and its distribution in assorted maize testers. Maydica 28:213–249

Peterson PA, Salamini F (1986) A search for active mobile elements in the Iowa Stiff Stalk Synthetic maize population and some derivatives. Maydica 31:163–172

Peterson T (1990) Intragenic transposition of *Ac* generates a new allele of the maize *P* gene. Genetics 126:469–476

Pisabarro AG, Martin WF, Peterson PA, Saedler H, Gierl A (1991) Molecular analysis of the *Ubiquitous* element system of *Zea mays*. Mol Gen Genet 230:201–208

Rhoades MM, Dempsey E (1982) The induction of mutable system in plants with the high-loss mechanism. Maize Genet Coop Newsl 56:21–26

Rhoades MM, Dempsey E (1983) Further studies on two-unit mutable systems found in our high-loss studies and on the specificity of interaction of responding and controlling elements. Maize Genet Coop Newsl 57:14–17

Russell WA, Penny LH, Guthrie WD, Dicke FF (1971a) Registration of maize germplasm inbreds. Crop Sci 11:140

Russell WA, Penny LH, Hallauer AR, Eberhart SA, Scott GE, Guthrie WD, Dicke FF (1971b) Registration of maize germplasm inbreds. Crop Sci 11:140–141

Schiefelbein JW, Furtek DB, Dooner HK, Nelson OE (1988) Two mutations in a maize *bronze-1* allele caused by transposable elements of the *Ac-Ds* family alter the quantity and quality of the gene product. Genetics 120:767-777

Schwarz-Sommer ZS, Gierl A, Cuypers H, Peterson PA, Saedler H (1985) Plant transposable elements generate the DNA sequence diversity needed in evolution. EMBO J 4:591-597

Seo B-S (1994) A transposable element in diverse corn lines, *Ubiquitous* (*Uq*): Allelism test. MSC thesis, Parks Library, Iowa State University, Ames, Iowa

Smith JSC (1986) Genetic diversity within the corn belt dent racial complex of maize (*Zea mays* L.). Maydica 31:349–367

Snedecor GW, Cochran WG (1967) Statistical methods, 6th edn. Iowa State Univ Press, Ames, Iowa, pp 250–253

Sprague GF (1946) Early testing of inbred lines of corn. J Am Soc Agron 38:107–117

Sprague GF (1986) Mutability in the *a-ruq, Uq* system in maize. Maydica 31:17–39

Sprague GF, McKinney HH (1966) Aberrant ratio: an anomaly in maize associated with virus infection. Genetics 54:1287–1296

Sprague GF, McKinney HH (1971) Further evidence on the genetic behavior of AR in maize. Genetics 67:533–542

Sughroue JR, Rocheford TR (1994) Restriction fragment length polymorphism differences among Illinois long-term selection oil strains. Theor Appl Genet 87:916–924

Walbot V (1986) Inheritance of mutator activity in *Zea mays* as assayed by somatic instability of the *bz2-Mu1* allele. Genetics 114:1293–1312

Walejko RN, Russell WA (1977) Evaluation of recurrent selection for specific combining ability in two open-pollinated maize cultivars. Crop Sci 17:647–651

Wessler SR (1988) Phenotypic diversity mediated by the maize transposable elements *Ac* and *Spm*. Science 242:399–405

Wessler SR, Baran G, Varagona MJ, Dellaporta SL (1986) Excision of *Ds* produces *waxy* proteins with a range of enzymatic activities. EMBO J 5:2427–2432