INTRODUCTION

Controlling elements in maize are transposable elements that cause insertion mutations, mediate chromosomal rearrangements and provide sites of chromosome breakage. Several distinct families of controlling elements have been identified, three of which have been studied in substantial detail genetically (for reviews, see McClintock, 1951, 1956b, 1965; Fincham and Sastry, 1974; Nevers and Saedler, 1977; Starlinger, 1980 and Fedoroff, 1982). Among the best characterized is the Activator-Dissociation family of elements that is responsible for the mutations at the Shrunken (Sh) locus described here (McClintock, 1951). Activator (Ac) is an element capable of autonomous transposition, while the Dissociation (Ds) element transposes only in the presence of the autonomously-transposing Ac element (McClintock, 1951). Ds was first identified and named for its ability to provide a specific site of chromosome breakage and
acentric-dicentric chromosome formation, a property that is also
manifested only in the presence of the Ac element (McClintock, 1946,
1947). Transposition of Ds to a locus affecting plant or kernel
morphology can result in a recessive mutant phenotype (McClintock,
1951, 1956b). Ds insertion mutations are stable in the absence of
Ac, but in its presence revert or further mutate both somatically
and germinally. Somatic mutation can give rise to phenotypically
altered sectors of cells within the organism (for illustrations, see
McClintock, 1965, and Fedoroff, 1982). Both the somatic and germinal
reversion of Ds mutations is commonly, but not invariably, associated
with the loss of the element from the locus. McClintock also
identified strains with Ds elements, which she designated as "non-
transposing", that behave as local mutagens (McClintock, 1952, 1953,
1954, 1955, 1956a). In these strains, the Ds element is characterized
by its ability to provide a site of chromosome breakage during
somatic development and by its ability to give rise to mutations
affecting nearby loci on one side or the other of the original site
of insertion, but not on both sides simultaneously (McClintock, 1952,
1953, 1954, 1955, 1956a). It is the non-transposing Ds elements that
are responsible for the mutations at the Sh locus whose molecular
characterization is described in the present communication.

The Sh locus in maize encodes the enzyme sucrose synthase, which
catalyzes the reversible conversion of sucrose to fructose and UDP-
glucose (Choure and Nelson, 1976). The Sh-encoded enzyme is the
major, but not the only sucrose synthase activity in immature endo-
sperm tissue (Choure and Nelson, 1976; Choure, 1981). There is a
second minor sucrose synthase that is enzymatically indistinguishable
from, and immunologically related to, the Sh-encoded enzyme (Choure,
1981). The minor sucrose synthase is encoded by a gene that is
distantly related to the coding sequence at the Sh locus (McCormick
et al., 1982). Mutations at the Sh locus substantially reduce, but
do not altogether abolish, endosperm starch biosynthesis. Several
mutant alleles of the Sh locus have been described whose origin is
associated with non-transposing Ds elements (McClintock, 1952, 1953,
1954, 1955, 1956a). The original unstable alleles are designated
sh-m5933, sh-m6233, and sh-m6258. There is also a derivative of
the sh-m6258 strain, designated sh-m6795, which represents a
recessive mutation derived from an unstable Sh revertant of the sh-
m6258 strain. The unstable alleles of the Sh locus arose in strains
containing a non-transposing Ds element just distal to the Sh locus
on the short arm of chromosome 9 (McClintock, 1952, 1953). All four
mutant alleles of the Sh locus are stable in the absence of the Ac
element, but revert to Sh alleles both somatically and germinally
in the presence of Ac. As judged by the location of the Ds-
associated site of chromosome breakage, neither the initial mutations
nor the reversion events are accompanied by transposition of the
element to a genetically distinguishable position (McClintock, 1953).
Revertants remain unstable, mutating to recessive alleles in the
presence of the Ac element (McClintock, 1955). The behavior of the