The Transposition Frequency of Tag1 Elements Is Increased in Transgenic Arabidopsis Lines

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Tag1 was identified as a highly active endogenous transposable element in transgenic Arabidopsis thaliana Landsberg erecta plants carrying the maize transposable element Activator (Ac). Here, we describe experiments designed to determine the basis for the high activity of Tag1. The frequency of transposition of Tag1 elements was compared in lines containing or lacking Ac transposase to assess the effect of Ac transposase on Tag1 activity. Three populations of nontransgenic plants, including nontransformed regenerants, were also analyzed. The high level of activity of Tag1 did not correlate with the presence or absence of Ac transposase but was significantly higher in transgenic lines. This result was maintained through at least six generations after transformation. These data suggest that Tag1 transposition is stimulated by processes that occur during the Agrobacterium transformation and that thereafter remain active. Two Tag1 elements are tightly linked in the Landsberg erecta genome and map to the lower arm of chromosome 1. Tag1 elements were found in only a few A. thaliana ecotypes but were present in four other Arabidopsis species.

INTRODUCTION

A number of mobile elements have been identified in Arabidopsis thaliana. Two of these, members of the Ta family (Voytas and Ausubel, 1988; Voytas et al., 1990; Konieczny et al., 1991) and Athila (Pelissier et al., 1995), are retrotransposon elements that use RNA intermediates in the transposition process. Until recently, the only other transposon characterized in A. thaliana was the Tat1 element (Peleman et al., 1992), however, it is still unclear whether Tat1 is an active element. Lack of a well-characterized transposable element system in A. thaliana led a number of groups to introduce heterologous elements into A. thaliana to establish a transposon-tagging system (Bancroft et al., 1992; Dean et al., 1992; Swinburne et al., 1992; Sundaresan et al., 1995). During the screening for Activator (Ac)-induced mutations in a population of Landsberg erecta plants, an unstable chlorate-resistant mutation (chl1-6) was identified. Gel blot analysis of DNA from chl1-6 with the previously cloned CHL1 gene (Tsay et al., 1993a) showed that it carried a 3.3-kb insertion, which is shorter than expected for an Ac element. Subsequent analysis identified the insertion as a new transposable element that was termed Tag1 (for tagging A. thaliana genes; Tsay et al., 1993b).

Tag1 had inserted into an intron in the CHL gene and generated an 8-bp duplication of the target site. This is a feature shared by Ac elements (Fedoroff et al., 1983). The element had 22-bp terminal-inverted repeats that contained A and G residues at positions 2 and 5 in the left repeat and complementary T and C residues in the right repeat. These residues are conserved in the short inverted repeats of the hAT superfamily of transposable elements (Warren et al., 1994). Somatic excision of Tag1 from the 5′ untranslated region of a cauliflower mosaic virus 35S promoter fusion driving β-glucuronidase demonstrated that Tag1 is an autonomous element in A. thaliana and tobacco (Frank et al., 1997). Recently, Tag1 has been used to tag a gene involved in organ separation in A. thaliana (Aida et al., 1997).

Tag1 was very active in the transgenic line in which it was first identified, excising from CHL1 to produce chlorate-sensitive revertants at a frequency of ~30% (Tsay et al., 1993b). Unstable mutations have not been commonly observed over many years of genetic analysis in the A. thaliana Landsberg erecta background; therefore, the high activity of Tag1 is surprising. We decided to investigate the activity of Tag1 elements in a large number of independent lines to determine whether Ac transposase affects Tag1 activity and whether Tag1 elements are equally active in nontransgenic and transgenic lines.

Tag1 is present in two copies in the Landsberg erecta genome but is not present in the other commonly used ecotypes, Columbia and Wassilewskija (Ws; Tsay et al., 1993b; Frank et al., 1997). To extend the use of Tag1 for tagging purposes, we have mapped Tag1 elements onto the restriction fragment length polymorphism map and analyzed...
the distribution of the element in different A. thaliana ecotypes and different Arabidopsis species.

**RESULTS**

**Comparison of Tag1 Activity in Transgenic Lines Expressing or Not Expressing Ac Transposase**

The Landsberg erecta transformants used to generate lines to study Tag1 element activity are summarized in Table 1. Transgenic lines expressing Ac transposase were generated from five transformants containing Ac elements cloned into the 5′ untranslated region of a streptomycin resistance fusion (SPT ::Ac and SPT ::Ac ∆Nael constructs) plus three transformants containing a stabilized Ac carrying a tobacco mosaic virus Ω 5′ untranslated leader (sAc ∆). sAc ∆ was made by cloning the Ω sequence into the Nael site of an ∆NaelAc element (S. Scofield, unpublished data). The Ω sequence has been shown to improve the translational efficiency of different mRNAs (Gallie et al., 1987). Seventy-eight transformants containing a hygromycin resistance fusion (Ds ::Ac) were examined for expression of the transposase (Tag1) activity. Transgenic lines not expressing a 35S–transcript were used in the analysis of Tag1 activity. The frequency of novel, inherited transposition events to avoid counting one transposition event twice. However, if excision was not associated with a reinsertion event, the number of Tag1 transposition events would have been underestimated.

Table 2 shows a comparison of the frequency of novel, independent Tag1 insertions in progeny from different transgenic lines. When a Tag1 transposition event was common to several siblings due to an early transposition event in the parent, this was only counted once. The percentage of plants carrying SPT ::Ac, SPT ::Ac ∆Nael, sAc ∆, and Hm Ds constructs or FCA transgenes that contained a novel Tag1 insertion varied from 10 to 100%. The Tag1 transposition frequencies observed in these transgenic populations are in line with the 30% reversion frequency observed for the original chlorate-resistant mutant (Tsai et al., 1993b). There was no obvious relationship between the frequency of Tag1 transposition and the activity of the different Ac derivatives. The four SPT ::Ac ∆Nael transformants showed an average germinal Ac excision frequency of 2.7% (Lawson et al., 1994), whereas SPT ::Ac transformants showed average frequencies five to 10-fold lower (Dean et al., 1992).

The three transformants carrying an sAc ∆ construct all showed a novel Tag1 reinsertion, making them the class of transformants showing highest Tag1 activity. The frequency of germinal Ds transposition when these sAc ∆ transposons were crossed to a Ds tester line was similar to that when the Ac transposase was provided by ∆NaelAc (Bancroft et al., 1992; A. Bhatt and C. Dean, unpublished results) and was in the range of 1 to 6%. T3 progeny from transformants carrying the Hm Ds elements, which had not been crossed to plants containing an Ac transposase source, showed levels of Tag1 activity similar to lines carrying the autonomous Ac elements. Similar levels of activity were also observed in T3 progeny from lines carrying FCA transgenes. Thus, the level of Tag1 activity is reproducibly high in the range of transgenic populations analyzed, but the high activity is not dependent on the presence of Ac transposase or Ac/Ds sequences.

**Tag1 Activity in Nontransgenic Lines**

Two hundred and ninety-eight recombinant inbred (RI) lines from a cross between Landsberg erecta and Columbia were also analyzed for Tag1 activity. These lines had not experi-
the ecotype, only a proportion of the RI lines showed hybridization (Figure 1). Successive generations of two
of 26 of their progeny (at T5, T6, or T7) were analyzed for Tag1 activity. For example, from transposant SPT::Ac:A17, three streptomycin-resistant (T6) individuals were selfed, and 19, 12, and 26 (totaling 57) progeny were analyzed.

Genic population in which to analyze Tag1 activity was analyzed by DNA gel blot analysis of an additional 123 individual Landsberg erecta plants. No new Tag1 insertions were detected in this population; thus, the frequency of Tag1 transposition was <0.8%.

The activity of Tag1 was clearly higher in the transgenic lines analyzed compared with the nontransgenic lines, suggesting that events occurring during either Agrobacterium transformation or the regeneration process stimulate Tag1 activity. To analyze the effect of tissue culture and regeneration on Tag1 activity, 65 independent Landsberg erecta plants were regenerated from root explants in the absence of selection for transformation. DNA was isolated and analyzed, as was done for the other populations. No new Tag1 insertions were detected, giving a frequency of Tag1 transposition at <1.5%. Thus, steps during Agrobacterium infection, selection for transformation, or T-DNA integration are likely to induce the high activity of Tag1.

### High Tag1 Activity in Transgenic Lines Is Maintained in Successive Generations

The presence of different Tag1 insertions in related progeny up to six generations after the transformation event suggested that Tag1 activity remained high and was not just induced during transformation. To analyze this further, Tag1 transposition was analyzed in two T4 plants that were then

<table>
<thead>
<tr>
<th>Plant Line</th>
<th>Generation Analyzed</th>
<th>No. of Plants</th>
<th>No. of Independent Tag1 Insertions</th>
<th>Frequency of New Tag1 Insertions (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPT::Ac:A17</td>
<td>T1</td>
<td>57</td>
<td>10</td>
<td>18</td>
</tr>
<tr>
<td>SPT::Ac:ΔNael-A3</td>
<td>T6 + T7</td>
<td>5</td>
<td>3</td>
<td>60</td>
</tr>
<tr>
<td>SPT::Ac:ΔNael-A8</td>
<td>T5</td>
<td>3</td>
<td>1</td>
<td>33</td>
</tr>
<tr>
<td>SPT::Ac:ΔNael-B3</td>
<td>T6 + T7</td>
<td>16</td>
<td>4</td>
<td>25</td>
</tr>
<tr>
<td>SPT::Ac:ΔNael-B10</td>
<td>T3</td>
<td>29</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>sAc1</td>
<td>T3</td>
<td>3</td>
<td>3</td>
<td>100</td>
</tr>
<tr>
<td>HmρDs</td>
<td>T3</td>
<td>78</td>
<td>14</td>
<td>18</td>
</tr>
<tr>
<td>FCA transgenes</td>
<td>T3</td>
<td>50</td>
<td>5</td>
<td>10</td>
</tr>
<tr>
<td>Landsberg erecta × Columbia RI lines</td>
<td>F10</td>
<td>118</td>
<td>2</td>
<td>1.7</td>
</tr>
<tr>
<td>Landsberg erecta plants</td>
<td>-d</td>
<td>123</td>
<td>0</td>
<td>&lt;0.8</td>
</tr>
<tr>
<td>Landsberg erecta regenerants</td>
<td>R1</td>
<td>65</td>
<td>0</td>
<td>&lt;1.5</td>
</tr>
</tbody>
</table>

a Five transformants carrying SPT::Ac and SPT::Ac:ΔNael constructs were analyzed. The prefixes A and B indicate the alternative orientations of the SPT::Ac construct relative to the NPTII fusion within the T-DNA: A, parallel; B, opposite.

b Individuals taken at the T6, T5, or T4 generation (with T1 being the primary transformant), which were identified as carrying Ac excisions (fully streptomycin resistant), were selfed; between one and 26 of their progeny (at T6, T5, or T4) were analyzed for Tag1 activity.

c Leaf material from pooled progeny of the 57 lines was used to isolate DNA for DNA gel blot analysis. Three independent transformants carrying sAc1, 78 independent transformants carrying HmρDs (which had not been crossed to an Ac transposase source), and 50 transformants carrying the FCA transgenes were analyzed in the T3 generation. The 118 Landsberg erecta × Columbia RI lines were the fraction of the 298 RI lines that contained Tag1. DNA was also isolated and analyzed from 123 individual Landsberg erecta plants that had not been transformed or used in previous genetic analysis and from 65 independent Landsberg erecta regenerants.

d-, not applicable.
crossed, and 74 of their “grandchildren” (T₆ plants) were used in DNA gel blot analysis of germinal Tag1 insertions. The results are shown in Table 3. The T₄ parents (transformants ΔNaelsAc[GUS]-1 and Hm⁸Ds-B1 [Bancroft et al., 1992] taken through three generations of selfing before the cross) carried a total of five Tag1 insertions. Multiple F₁ plants were generated and selfed, and F₂ seed was collected. Plant material from bulked F₃ families was used to assess the genotype of the F₂ plants. The numbers of independent, novel Tag1 insertions per number of F₂ plants analyzed from each F₁ generation are shown in Table 3. The frequency of new insertions per F₂ plant varied from 0 to 150%, with the 150% resulting from one of the two F₂ plants analyzed carrying two new insertions. Overall, there were 23 independent insertions in 74 F₂ plants that were not present in the T₄ parents. These transposition events will have occurred in the T₅ generation and been germinally transmitted to the T₆ progeny. Thus, we can estimate the frequency of Tag1 transpositions in the T₅ generation to be 23 of 74, or 31%.

Table 3. Tag1 Activity in the T₅ Generation

<table>
<thead>
<tr>
<th>F₁ Plant</th>
<th>No. of F₂ Individuals Analyzed</th>
<th>No. of Novel Tag1 Insertions</th>
</tr>
</thead>
<tbody>
<tr>
<td>st8</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>gp17</td>
<td>8</td>
<td>2</td>
</tr>
<tr>
<td>gp5</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>gp18</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>gp12</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>st1</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>sb3</td>
<td>4</td>
<td>2</td>
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<tr>
<td>gp11</td>
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<tr>
<td>gt19</td>
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<td>sp4</td>
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<td>gb12</td>
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</tr>
<tr>
<td>sb5</td>
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<td>1</td>
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<tr>
<td>gh22</td>
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<td>3</td>
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<td>gp14</td>
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<td>st7</td>
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<td>0</td>
</tr>
<tr>
<td>st10</td>
<td>2</td>
<td>1</td>
</tr>
</tbody>
</table>

*F₁ plants were from a cross between two T₄ plants carrying an Ac transposase source and a Ds element ΔNaelsAc[GUS]-1 and Hm⁸Ds-B1, respectively; Bancroft et al., 1992). Fully streptomycin-resistant (resulting from a germinal Ds excision) F₂ seedlings were selected from 20 F₁ plants.

*Plant material from bulked F₃ families was used to assess the genotype of the F₂ plants. The number of independent, novel Tag1 insertions per number of F₂ plants analyzed from each F₁ generation is shown.

Figure 1. Analysis of Tag1 Transposition in the Landsberg erecta and Columbia RI Line 25.

Genomic DNA was isolated from individual F₃ and F₁₀ plants, pooled F₁₀ plants, and parental Landsberg erecta (L. erecta), digested with HindIII, and used to generate a DNA gel blot. The blot was probed with the internal 1.4-kb EcoRI fragment of Tag1. Using this digest and probe combination, each Tag1 transposition event would result in two novel cross-hybridizing HindIII fragments. The five HindIII fragments that cross-hybridized with Tag1 in the progenitor are indicated by asterisks. The second and third largest fragments run as a doublet. HindIII fragments from transposed Tag1 elements are indicated by open arrowheads. Numbers at left indicate the lengths (in kilobases) and positions of λ HindIII fragments.
**Map Position of Tag1 Elements**

The Landsberg erecta genome carries two copies of Tag1 (Frank et al., 1997). Because Tag1 was absent from the Columbia ecotype, the elements could be mapped using the Landsberg erecta/Columbia RI lines. Apart from new Tag1 transpositions in RI line 25 (described above), only two other RI lines showed a pattern that differed from the Landsberg erecta parent. RI line 385 lacked two and RI line 398 lacked one of the HindIII restriction fragments that hybridized with Tag1. Neither of these lines showed new Tag1 reinsertion events, so these events were not scored as transpositions. It is difficult to distinguish Tag1 excisions not accompanied by reinsertions from recombination events. However, we can conclude that the two Tag1 elements cosegregated in 116 (of the 118 showing any hybridization with Tag1) RI families, indicating that they are tightly linked in the A. thaliana genome. The Tag1 elements mapped to the lower arm of chromosome 1 (Figure 2). The CHL1 locus that was mutated by a Tag1 insertion is on the upper arm of chromosome 1, ~90 centimorgans away from the donor site (Tsay et al., 1993b).

**Distribution of Tag1 Sequences in Different A. thaliana Ecotypes and Arabidopsis Species**

In a previous study (Tsay et al., 1993b), it was reported that Tag1 sequences were present in A. thaliana ecotype Landsberg erecta but absent in the ecotypes Columbia and Ws. We have extended this study and looked at a large number of A. thaliana ecotypes and species for sequences with homology to Tag1. We have included ecotypes C24 and Nossen-0 (No-0), which have been extensively used for T-DNA and transposon-tagging experiments (Koncz et al., 1989; Fedoroff and Smith, 1993). Tag1 sequences were present in Landsberg erecta, S96, Dijon-G, Graz, and No-0 (Figure 3). Dijon-G carries the same Tag1 fragments as Landsberg erecta carries. S96 shows three of the five fragments present in Landsberg erecta, whereas Graz and No-0 have two hybridizing fragments; one of these (the internal BglII fragment) is common to those present in Landsberg erecta. These ecotypes therefore appear to contain one copy of a Tag1 element. A different accession of No-0 has been found to carry no Tag1 hybridizing fragments (N. Crawford, unpublished results). Tag1 cross-hybridizing fragments were not present in the following A. thaliana ecotypes: Warschau-1, C24, Allerup-0, Stockholm, Enkheim, Osthammar, Bensheim, Estland-0, Wilna/Litauen, Kopenhagen, Niederenz, RLD, Tenela, and Cape Verde Islands (data not shown for all ecotypes). A screen of an additional 35 ecotypes has shown Tag1 elements present in 16 of them (M. Frank and N. Crawford, unpublished results).

The four Arabidopsis species tested were A. wallachii, A. griffithiana, A. korshinskyi, and A. suecica. They all had numerous Tag1 cross-hybridizing fragments, indicating that they have multiple Tag1 elements (Figure 3). The BglII enzyme used in this analysis yields both internal and flanking fragments when hybridized with the internal EcoRI fragment of Tag1. We interpret the large number of fainter fragments in the A. griffithiana and A. suecica lanes to represent different flanking fragments. Further analysis of A. wallachii and A. griffithiana DNA digested with EcoRI (which should yield only internal fragments) confirmed this interpretation because only two and three EcoRI fragments hybridized, respectively, with the internal 1.4-kb EcoRI fragment, compared with the two found in Landsberg erecta (data not shown). The faint hybridization signal of some of the fragments in A. griffithiana and A. suecica may reflect sequence divergence of different members within this transposon family. The restriction fragments hybridizing with Tag1 were similar in A.
The presence of multiple Tag1 elements in the Arabidopsis species and the low copy number or absence from most of the A. thaliana ecotypes suggest that Tag1 elements have been lost from the genomes of most of the A. thaliana ecotypes, perhaps through a low frequency of reinsertion after excision.

**DISCUSSION**

Tag1 was first identified as an active transposable element in a population of transgenic A. thaliana (Landsberg erecta) plants containing a maize Ac element. The frequency of excision of Tag1 from the CHL1 locus (where it was first detected) was extremely high, with 30% of the chlorate-resistant individuals reverting to chlorate sensitivity. The goal of this study was to investigate the basis for the high activity of Tag1.

Tag1 activity was similar in a large number of transgenic lines derived from 136 independent transformants carrying either active Ac or sAc elements (expressing Ac transposase), Ds elements (not expressing Ac transposase), or FCA transgenes. This showed that the high activity of Tag1 was not caused by the presence of Ac transposase or any sequences associated with Ac or Ds elements. However, the frequency of Tag1 transposition was five- to 125-fold higher in transgenic lines compared with nontransgenic plants. All of the Landsberg erecta transgenic lines had been through a procedure involving Agrobacterium transformation of root explants and kanamycin selection. The T2 seeds from the selfed T1 primary transformants were then germinated on kanamycin-containing medium, and seedlings were grown on this medium until large enough to be transplanted to soil. To begin to address at which stage of this procedure Tag1 was activated, we analyzed the frequency of Tag1 transposition in Landsberg erecta plants that had been regenerated from root explants but that had not experienced Agrobacterium or selection for transformation. Tag1 activity was 1.5% in these plants, so the increased frequency of Tag1 transposition appeared to be the result of either Agrobacterium transformation and T-DNA integration or antibiotic selection. Once activated, the Tag1 elements continued to transpose through successive generations, at least until the T6 generation.

Transposable elements have been shown to be activated in maize and tobacco by tissue culture, plant disease, UV light, and γ irradiation (Dellaporta et al., 1984; Peschke et al., 1987; Walbot, 1988, 1992; Peschke and Phillips, 1991; Hirochika, 1993). It is postulated that these stresses activate transposable elements, thus generating allelic variation that may help the organism in new situations. The activation of Tag1 in transgenic A. thaliana lines appears to represent another example of this type of activation. It is not difficult to envisage how Agrobacterium transformation and T-DNA integration might activate stress responses, which would lead to transposable element activation.
Tag1 elements were tightly linked and mapped to the bottom of chromosome 1. The reported mutation caused by Tag1 is at the CHL1 locus, which is on the top arm of chromosome 1, ~90 centimorgans from the donor site. Many more transposition events will have to be analyzed before it becomes clear whether Tag1 shows a tendency to transpose to linked sites in the genome. Analysis of the pattern of Tag1 transposition and the factors that affect Tag1 transposition should help in optimizing strategies that use Tag1 elements as effective insertional mutagens in Landsberg erecta.

The absence of Tag1 elements in ecotypes C24 and WS means that nontagged mutants from T-DNA tagging experiments in these ecotypes cannot be attributed to activity of Tag1 elements. A number of mutations identified in Landsberg erecta populations that contained transposed Ac or Ds elements but that were not Ac- or Ds-tagged were analyzed to determine whether they were tagged with Tag1 elements. None of the five mutants analyzed cosegregated with Tag1 elements (A. Bhatt and C. Dean, unpublished results). It is possible that other endogenous transposons or retrotransposons could account for the background mutations in such experiments.

Analysis of the hybridization pattern of Tag1 elements contributes to our understanding of the relationship of the A. thaliana ecotypes and Arabidopsis species. The identical hybridization pattern of Tag1 elements in Landsberg erecta and Dijon-G suggests that these ecotypes may have a common origin. Based on a study of chloroplast DNA restriction sites, Price et al. (1994) suggest that A. suecica is more closely related to A. thaliana than to A. griffithiana or A. wallichii. However, the pattern of restriction fragments hybridizing with Tag1 suggests a different relationship, with A. suecica and A. griffithiana being more closely related to each other than to A. thaliana. Why such a high proportion of A. thaliana ecotypes lacks Tag1 sequences is not clear. It may be due to the loss of the elements, perhaps by excision events not associated with reinsertion. This may be the explanation for why different No-0 accessions carry different Tag1 complements. The study of Tag1 and related elements will reveal much more about the different Arabidopsis species and ecotypes and will enable Tag1 to be exploited more widely as an insertional mutagen.

**METHODS**

**Plant Lines**

The transgenic lines used in the study have been described elsewhere. All of the plants were derived from Agrobacterium tumefaciens transformation of root tissue (Valvekens et al., 1988) of Arabidopsis thaliana ecotype Landsberg erecta. The lines containing an active, mobile Activator (Ac) element carried either a wild-type autonomous Ac cloned into the streptomycin resistance gene (Dean et al., 1992) or a modified autonomous Ac element, termed AcΔNaeI, in which 537 bp (between NaeI restriction sites) had been deleted from the 5' untranslated leader of the Ac transposase gene. This deletion resulted in higher somatic and gamential excision of the Ac element in A. thaliana (Lawson et al., 1994). The lines containing a stabilized Ac element (sAc), which still had an active Ac transposase source, carried either ΔNaeI sAc (Bancroft et al., 1992) or an sAcΔI element in which 82 bp of the 5' untranslated sequence of the tobacco mosaic virus coat protein (termed ΔI sequence) had been cloned into the NaeI site of ΔNaeI sAc. The lines containing a nonautonomous Disso-}

_The different Arabidopsis ecotypes and species were acquired from the AIS collection held by A.R. Kranz (Fachbereich Biologie Universität Frankfurt/Main, Germany) and are now at the Nottingham Stock Centre (Nottingham, UK)._
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