Sequence Arrangement in Satellite DNA from the Muskmelon

ARNOLD J. BENDICH and WILLIAM C. TAYLOR
Departments of Botany and Genetics, University of Washington, Seattle, Washington 98195

ABSTRACT

Two fractions of a satellite DNA from the muskmelon (Cucumis melo L.) isolated as a unimodal peak from CsCl gradients, differ in melting properties and complexity as estimated by reassociation kinetics. At 49.8°C, all of the low melting fraction was denatured and all of the high melting fraction was native. There were almost no partially denatured molecules detected in the electron microscope at this temperature. This observation provides direct evidence that the two fractions are not closely linked. We conclude that satellite I, the high t_m, low complexity fraction, exists as a 600-nucleotide sequence in blocks of at least 67 tandem repeats. Since the complexity of the low melting fraction, satellite II, is greater than the size of the molecules in our assay, we can only say that the minimum size of each unit of satellite II is 2.5 × 10^5 daltons. It is unlikely that any spacer sequences are interspersed with either satellite.

Sequences homologous to those of satellite I were also shown to be present as a minor fraction on 4900 nucleotide pair fragments with main band DNA density. These long main band fragments probably contain in addition at least two repeated sequence elements unrelated to satellite I since they aggregate (form large network structures) when reassociated. Coaggregation of sheared 3H-satellite I with long main band DNA could not be attributed to contamination of main band with long satellite DNA. We interpret the results as an observation of a recently created family of tandemly repeating sequences whose members are beginning to be scattered throughout the genome.

We discuss how the aggregation technique may be generally useful for assessing linkage between a minor and a major DNA fraction when both fractions may be present in the initial DNA preparation. Applications for the technique include the search for DNA sequences in the nucleus which are homologous with chloroplast DNA and for Agrobacterium tumefaciens DNA in the nuclei of plant cells transformed to the tumor phenotype by the bacterium.

Satellite DNAs isolated from density gradients are generally simple sequence DNA. These repeating units may be almost exact replicas, as in the case of satellite I of the crab (19), or they may be a collection of sequences which are sufficiently similar to reanneal under standard conditions but which exhibit a fair degree of divergence. Mouse satellite is the classic example of the latter kind of satellite (10). Peacock et al. (16) and Gall and Atherton (12) have reported that the satellites of Drosophila melanogaster and Drosophila virilis occur as large blocks of tandem repeats. Kram et al. (14), however, concluded that spacer DNA is interspersed among the repeating satellite sequences in D. melanogaster. Rice (17) viewed mouse satellite DNA as a basic 50-nucleotide sequence tandemly repeated in stretches averaging 750 nucleotides which are interrupted by spacer sequences of about 60 nucleotides.

The few plant satellite DNAs which have been investigated carefully are composed of at least two components which exhibit different melting properties and different complexities as estimated from reassociation kinetics (2, 7, 18; our unpublished results). We previously characterized a dense satellite DNA which represented 30% of total DNA from muskmelon (Cucumis melo L.) satellite I. The satellite exhibited a sharp, unimodal peak in both neutral and alkaline CsCl gradients. Its density in neutral CsCl was 1.706 g/cm^3 compared with a main band density of 1.692 g/cm^3; these values were in good agreement with those published earlier (13). In spite of its sharp banding profile in CsCl, the satellite proved to be heterogeneous. It melted as two fractions: the lower melting two-thirds had a t_m, 8°C below that of the higher melting one-third. Analysis of reassociation kinetics revealed two major components reassociating with ideal second order kinetics: a fast reassociating component comprising 37% of the satellite, and a slower one comprising 44%. The fast component was high melting and had a kinetic complexity of 3.7 × 10^9 daltons or about 600 nucleotide pairs, and the slower, low melting component had a complexity of 1.1 × 10^6 daltons. The number of copies of the fast and slow components in this dense satellite is estimated to be 1.8 × 10^6 and 72, respectively. The reassocated satellite contained very little base mispairing since its t_m was nearly that of the native form. Separation of the satellite into two fractions was achieved in CsSO_4 density gradients with Ag^+ or Hg^++. A later publication by Sinclair et al. (18) confirmed most of the above data. They suggested that the two components were linked since the two peaks obtained from their Ag^+-CsSO_4 gradients contained neither pure fast nor slow reassociating components nor pure melting fractions.

We decided to assess linkage directly by looking for partially denatured long molecules in the electron microscope. Since melting profiles of the two fractions are sharp and there is an 8°C difference in their t_m values, we should be able to find a temperature at which all of the low melting fraction has denatured, but none of the high melting fraction has begun to melt. If the two fractions are linked, we should see partially denatured molecules at this temperature. But if they are not linked, we should see no, or very few, partially denatured molecules at a temperature intermediate between the t_m of the two fractions. From the data, inferences may be drawn concerning the possible existence of spacer sequences.

Abbreviations: t_m: temperature at which half of the DNA has denatured; C_l: concentration in mol nucleotide x time in sec/liter.

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2 Present address: Department of Biology, University of California, San Diego, La Jolla, Calif. 92137.

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Satellite DNA sequences are recognized and are separated from bulk DNA in density gradients only when the satellite sequences constitute a large portion of the DNA fragments bearing them. If DNA fragments exhibiting main band density contain short lengths of sequence homologous to the satellite, then these sequences would normally be discarded in the analysis of "satellite DNA." However, investigation of such sequences might be useful in elucidating the manner in which satellite DNA may be useful to the cell. A study of satellite-homologous sequences which are interspersed with sequences of main band density might be useful for inferring the evolutionary history of satellite DNA. We report on experiments which detect short satellite sequences present on larger main band fragments.

MATERIALS AND METHODS

DNA Preparation and Melting Profile. Satellite DNA used to assess linkage was prepared by banding in successive CsCl gradients as previously described (2) except that the DNA was not intentionally sheared and was handled carefully to minimize shearing. DNA used for aggregation was extracted with detergent and treated with chloroform, ribonuclease, pronase, and ethanol, as previously described (2). The melting profile of the DNA was determined in the same medium used for spreading the DNA for electron microscopy. Measurements were made in a Gilford 2400 recording spectrophotometer equipped with a thermal programer accessory.

Electron Microscopy. DNA was spread for electron microscopy using a modified Kleinschmidt procedure which employed formamide to increase contrast and to lower denaturation temperatures, similar to the method outlined by Davis et al. (9). The spreading solution (0.2 μg/ml of DNA in 60% formamide and 0.1 M tris-HCl, pH 8.6) was incubated in a Lauda water bath for 10 min. Then 1% Cyt c was added to a final concentration of 0.02% and the incubation was continued for another 10 min. Fifty μl were spread over a hypophase of 30% formamide and 10 mM tris. The DNA was picked up on grids coated with a 3.5% Parlodion film, stained 30 sec with uranyl acetate (5 × 10⁻⁵ in 90% ethanol), and shadowed with platinum.

Micrographs were taken of randomly selected molecules in a Philips EM 201 electron microscope. Length measurements of molecules were made with a GP3 Graf-pen digitizer integrated with a Hewlett-Packard 9820-A desk calculator. Length calibrations were made with φX174 double strand replicative form II (RFII) (supplied by E. T. Young) and φX174 single strand RF DNA (supplied by W. L. Fangman).

Aggregation Assays. For aggregation assays, DNA samples in 5 mM tris-HCl buffer (pH 8), 0.2 M NaCl were denatured at 100 C for 5 min and incubated at 58 C (25 C below the Tm for main band DNA). The samples were then quickly cooled to 0 C, diluted to 0.2 ml with incubation buffer, and centrifuged at 4 C for 30 min at 35,000g. After removing the supernatant, the aggregate pellet was resuspended in 0.195 ml incubation buffer and both fractions were again denatured at 100 C and quickly cooled to 0 C. Following absorbance determinations, radioactivity was measured in toluene-Triton X-100 (2:1) with Omnifluor as the scintillant.

RESULTS

The thermal denaturation profile of satellite DNA in 0.1 M tris-HCl (pH 8.6) and 60% formamide showed the same bi-phasic form (Fig. 1) as found in other solvents (2, 18). Sixty per cent of the satellite melted with a Tm = 45.3 C; 40% melted with a Tm = 54.1 C. There was also a temperature range between the two fractions in which there was almost no hyperchromic shift: only 2% of the total hyperchromicity occurred from 50 to 52 C. The denaturation profiles of the two fractions were quite sharp, with the first fraction melting over an 8 C range and the second over a 3 C range.

Measurements of unselected molecules showed that a portion of the molecules from three of the temperature points were partially denatured (Table I). However, only one out of 241 molecules measured at 49.8 C was partially denatured. This molecule represented 1.1% of the total mass of DNA. All of the other molecules in the 49.8 C sample were either native or completely denatured. There was a reasonably good agreement between the per cent denatured DNA as measured in the electron microscope and the per cent hyperchromicity as determined in the spectrophotometer. At 49.8 C, 54% of the mass of DNA was in denatured form, which was close to the 59% hyperchromicity seen in the optical melt.

A representative field of DNA spread at 49.8 C is shown in Figure 2a. All of the molecules are either completely native or denatured. The long, native molecule is 7 μm (Fig. 2a1) and the

Table I. Fraction of DNA Molecules with Partially Denatured Regions

<table>
<thead>
<tr>
<th>Temperature °C</th>
<th>Molecules Measured</th>
<th>Partially denatured</th>
<th>Denatured</th>
<th>Hyperchromicity</th>
</tr>
</thead>
<tbody>
<tr>
<td>44.0</td>
<td>223</td>
<td>30</td>
<td>25</td>
<td>17</td>
</tr>
<tr>
<td>48.0</td>
<td>137</td>
<td>26</td>
<td>40</td>
<td>54</td>
</tr>
<tr>
<td>49.8</td>
<td>241</td>
<td>1.1</td>
<td>54</td>
<td>59</td>
</tr>
<tr>
<td>52.0</td>
<td>153</td>
<td>41</td>
<td>62</td>
<td>66</td>
</tr>
</tbody>
</table>

1Calculated as length of molecules with partially denatured regions divided by the total length of all molecules
2Percent total length which is denatured
3Data from spectrophotometer (Fig. 1)

![Figure 1. Melting curve of purified satellite DNA done in the spectrophotometer in the same conditions as is used for spreading the DNA for electron microscopy (0.1 M tris [pH 8.6] and 60% formamide). Arrows indicate temperature points analyzed in Table I.](image-url)
longest denatured molecule is 7.5 µm (Fig. 2a). A partially denatured molecule, 3.9 µm long, from the 48 C point is shown in Figure 2b. Both ends are partially denatured and there is a 2.2-µm denatured region near its center. A partially denatured molecule spread at 52 C can be seen in Figure 2c. There is a 1.7-µm denatured region near its center and it is 4.7 µm long.

DNA spread at 55.2 C contained almost no native DNA molecules. Many molecules were partially denatured at multiple regions which caused them to appear tangled and therefore impossible to measure accurately. We therefore excluded this point from the quantitative analysis, but it fit the general pattern of the other four points.

About 30% of muskmelon DNA fragments collect in CsCl gradients at 1.706 g/cm³. However, there may yet be additional short lengths of satellite sequences interspersed with main band DNA which sediment at main band density. In order to test this possibility, ³H-labeled sheared satellite DNA was added to excess unlabeled long DNA and aggregation assays were performed (Table II). The per cent of labeled main band DNA found in the aggregate was slightly less than that of unlabeled main band DNA in the aggregate (line 1). This is to be expected since the short labeled fragments would have less DNA contiguous with reassociating regions than would the longer unlabeled fragments. PS8 bacteriophage DNA did not form aggregates in the absence of excess main band DNA (line 5). Since there presumably exists no DNA sequence homology between PS8 and muskmelon, no ³H-PS8 DNA would be expected to join a main band aggregate via heteroduplex formation. Therefore, the 5% of ³H-PS8 DNA which pelleted with the main band aggregate was due to nonspecific association (line 3).
Whereas \( ^3\)H-satellite DNA did not form aggregates in the absence of main band DNA (line 4), 25\% of the \( ^3\)H-satellite DNA did aggregate with excess long main band DNA (line 2). The \( ^3\)H-satellite DNA also formed aggregates in the presence of an excess of long unlabeled satellite DNA (line 6). There are two possible reasons for the observed aggregation of satellite with excess main band DNA. Either there are contaminating long satellite molecules present in the main band preparation, or there are short satellite sequences covalently linked with long molecules of main band density. To distinguish between these alternatives, we sought to determine how much contaminating satellite DNA would have to be in our main band preparation to account for the observed aggregation. Contamination was simulated by mixing sheared \( ^3\)H-satellite with long satellite DNA and aggregation was assayed (lines 7–9). With respect to long DNA, the \( C_0 \) values in lines 7 through 9 are 7.8, 2.6 and 0.8\%, respectively, of that in line 2. From a comparison of \( ^3\)H-aggregation in lines 2 and 7, it is evident that more than 7.8\% of the main band would have to be satellite, if the observed \( ^3\)H-aggregation in line 2 were due to contamination. To assess the purity of the main band preparation, a mixture was made such that satellite represented 2.8\% of the total DNA, and this mixture was banded in CsCl (Fig. 3). It is clear that any contamination of main band with satellite is well below 2.8\% and probably below 1\%. Therefore, the contamination alternative is ruled out and short satellite sequences must be scattered among the sequences with main band density. Any trace contamination of the unlabeled main band with satellite DNA would lead to reassOCIation of labeled and unlabeled DNA strands, but these would remain in the supernatant.

**DISCUSSION**

**Are the Two Satellite DNAs Linked?** The dense satellite of the muskmelon is composed of two components, a fast reassociating, high melting part with a complexity of \( 3.7 \times 10^6 \) daltons and a slower reassociating, low melting part with a complexity of \( 1.1 \times 10^6 \) daltons. Since there is almost no mispairing in the reassociated satellite, the kinetic complexity may be taken to represent the sequence complexity, as is the case for viral or bacterial DNA. To determine if these two components are linked, satellite DNA was prepared for electron microscopy at a range of temperatures which covered the denaturation of both components. The optical melting profile (Fig. 1) shows a temperature range of several degrees in which there is little or no hyperchromic increase. DNA spread in this temperature range should show all of the low melting fraction to be single-stranded and all of the high melting DNA to be double-stranded. If the two fractions are not linked, then each molecule should contain only pure low melting or pure high melting DNA; only completely single-stranded or completely double-stranded DNA with no partially denatured molecules should be visualized. Alternatively, if the two components are linked, there will be partially denatured molecules at all temperatures. DNA spread in the transition temperature range will be partially denatured since the low melting component, which will be single-stranded, will be linked to the high melting component, which will be double-stranded. A proportion of the DNA spread at temperatures above or below the transition range should be partially denatured, whether or not the two components are linked.

Our results provide direct evidence that the two satellite components are not linked (Table 1). Only 1 molecule out of 241 measured at 49.8 C was partially denatured. The fact that 54\% of the total mass of DNA was single-stranded at this temperature fits well with the observation that the low melting fraction comprises 59\% of the satellite.

Sinclair et al. (18) suggested that the two satellite fractions...
were linked to each other or to a third, heterogeneous melting fraction of the satellite. This was inferred because they were able to enrich for each homogeneous fraction in AgNO₃-Cs₂SO₄ gradients but neither fraction could be obtained in pure form. However, whereas their AgNO₃-Cs₂SO₄ gradients did contain two major peaks, the peaks were not completely resolved and cross-contamination would inevitably result.

On the basis of our results, we can draw the following conclusions about the arrangement of sequences of the two satellite components which we will now call satellites I and II (Table III). The complexity of the satellite I is 3.7 × 10⁹ daltons which is much shorter than the double-stranded molecules observed at 49.8 C. These ranged from 1.6 × 10⁶ to 2.5 × 10⁷ daltons. Therefore, many copies of this sequence must be present on the DNA fragments we observed. Satellite I, then, exists as a 600-nucleotide sequence in blocks of at least 67 tandem repeats. Since there are about 1.8 × 10⁹ copies of this satellite in the muskmelon genome, it is possible that satellite I is comprised of blocks of much more than 67 tandem repeats.

Satellite II has a complexity of 1.1 × 10⁹ daltons and is estimated to be present in 72 copies per genome. Since the complexity is larger than the size of the molecules in our assay, we can only say that the minimum size for each unit is about 2.5 × 10⁵ daltons. We cannot say whether satellite II exists as units 1.1 × 10⁹ daltons in length or as subdivided units. We also cannot determine the arrangement of the 72 copies of this satellite. The possibility must be considered that spacer sequences exist interspersed among the sequences already described. The fact that the t₀ of reassociated satellite DNA is essentially the same as that of the native form makes it unlikely that any other sequences are interspersed with the repeating satellite units. Any such spacer sequences would themselves have to be arranged with a precise periodicity and repeating sequence and would have to be shorter than the limit of visual detection (about 75 nucleotides). There was no evidence at the 49.8 C point that denatured molecules containing the low melting sequences were held together at short regions which one would expect if there were spacers with a high t₀. Molecules containing high melting sequences showed no evidence of a low melting spacer. In this case, one would expect the otherwise native, high melting molecules to appear kingly if they contained low melting spacers too short to be visible as denaturated regions.

Are There Satellite Sequences in the Main Band? Britten first described the aggregation phenomenon and suggested that in order to form such networks there probably is a requirement for an average of more than two regions per strand capable of pairing with complementary regions on other strands (3). We have seen in the electron microscope multibranched structures with broad bean (unpublished results) and pea DNA (1) containing hundreds to thousands of interlocking strands. Thompson has characterized pea DNA aggregates (21). When aggregates are formed with DNA incubated at a Cₜ value insufficient to allow nonrepeated muskmelon sequences to begin to reassociate, as is the case in Table II, it seems likely that the interacting strands contain an average of two or more repeated sequence elements.

With respect to H-satellite DNA only, the Cₜ value in Table II, line 2 was sufficient for all of satellite I to reassociate, but for little or no satellite II to reassociate. It is therefore likely that the labeled satellite DNA which did aggregate with main band DNA was mostly, if not exclusively, satellite I. We will assume for the remainder of our discussion that all of the H-satellite in Table II, line 2 which participated in aggregation was satellite I.

We have demonstrated that the aggregation of satellite DNA with main band is due to the presence of short satellite sequences interspersed in the main band. The length of sequence in the main band which is complementary to satellite I must be short compared to the 4900-nucleotide main band fragments used. Furthermore, these short satellite sequences must be distributed such that they comprise a minor fraction of any given long main band fragment. Any main band fragment containing more than a minor fraction of satellite sequences would be found in the dense side of the main band peak which was discarded. The most likely situation is that a short stretch of satellite I sequence is present on some 4900-nucleotide main band fragments which contain at least two repeated sequence elements unrelated to satellite I.

When sheared H-satellite I was allowed to reassociate with long main band DNA in excess, a given labeled strand could have formed a duplex either with a complementary labeled strand or with a complementary region of an unlabeled main band strand. If the concentrations of H-satellite I strands and unlabeled complementary regions were equal, the majority of resultant satellite I duplexes should contain two labeled strands. In such a competition, short strands should find one another in solution more easily than one short strand finds a small complementary region on a long strand, either free or part of a network. In Table II, line 2 the mass ratio of input H-satellite I to main band DNA found in the aggregate was about 1% (1 part satellite of which 37% is satellite I, plus 100 parts main band of which half aggregated). Since at least half of the reassociated satellite I strands were found in the aggregate pellet, the concentration of sequences homologous to satellite I in the aggregated main band should be >1%. The concentration in the nonggregated main band should be much lower. From the specific radioactivity, we calculate that 0.4% of the main band DNA which aggregated is composed of sequences homologous to satellite I. This value of 0.4% must be well below the saturation level because of the above mentioned competition.

We may now estimate the number of 600-nucleotide units of satellite I which are scattered throughout the genome. The haploid DNA content of muskmelon is 6 × 10¹¹ daltons, including 70% main band of which half or about 2 × 10¹⁰ daltons formed aggregates. If we take 1% as a minimal estimate of satellite-homologous sequences in the aggregatable main band, we have 2 × 10⁹ daltons which should be divided by the mass of a 600-nucleotide pair unit: 3.7 × 10⁴ daltons. Therefore, in addition to 1.8 × 10⁹ tandemly repeating units in satellite I, at least 5000 or another 3% are dispersed elsewhere in the genome.

We wish to point out the utility of the aggregation technique in the general problem of assessing linkage between a minor and a major DNA fraction when both fractions may be present in the initial DNA preparation. In the purification of the major fraction, it would be difficult to exclude contamination rigorously from the minor fraction at a level below 1%. If standard DNA-DNA hybridization techniques employing hydroxyapatite, filter-bound DNA, or single strand-specific nucleases were used to score duplexes formed between the labeled minor fraction and unlabeled major fraction DNAs, a level of hybridization attributable to 1% of the major fraction could be due entirely to putative contamination. The hybridization will occur regardless of linkage of the fractions. However, using the aggregation assay

### Table III. Properties of Muskmelon Satellite DNA

<table>
<thead>
<tr>
<th>Complexity</th>
<th>Repeats/Length</th>
<th>MTP</th>
<th>Copies/Genome</th>
</tr>
</thead>
<tbody>
<tr>
<td>Satellite 10⁹ daltons</td>
<td>1900</td>
<td>1.2 × 10⁶</td>
<td>20</td>
</tr>
<tr>
<td>Satellite II</td>
<td>1.07</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Haploid genome size of muskmelon is 6 × 10¹¹ daltons (18).

2 Most of the satellite in the pellet is in duplex form, since 66% of purified, sheared H-satellite I coaggregating with long main band DNA was resistant to digestion by the single strand-specific nuclease, SI (unpublished data).
under conditions in which the minor fraction alone does not aggregate, only labeled DNA which anneals with homologous sequences *covalently linked* to the aggregating major fraction will be scored. The technique can therefore be used to identify such linkage despite a moderate level of contamination from unlinked minor fraction sequences, as is evident from the experiments in Table II. The problem of identifying "a needle in a haystack" should be simplified by the technique.

An application for which the aggregation technique seems particularly suitable is the assessment of DNA sequences in the nucleus which are homologous with chloroplast DNA. The observation that ribosomal RNA from chloroplasts hybridizes with a DNA prepared from nuclei has been interpreted as evidence for such sequences (20). Chloroplast DNA linked with nuclear DNA at a level below 1% should be detectable, assuming chloroplast DNA alone does not aggregate readily. A second application would be in the search for *Agrobacterium tumefaciens* DNA sequences in the nuclei of plant cells transformed to the tumor phenotype by the bacterium (15). Varmus and associates (22, 23) have used the aggregation technique to show that the incoming tumor virus genome may be found in the nucleus of duck cells first in an unintegrated form, later in an integrated form, and may be prevented from integrating into host DNA by ethidium bromide.

DNA sequences of intermediate repetition frequency are found interspersed with nonrepetitive sequences in all animals which have been studied, and in most cases there is a major class of interspersed repetitive sequences of size 300 to 500 nucleotide pairs (8). However, the question of how repeated sequences come to be scattered throughout the genome has received little experimental investigation. From theoretical considerations, Britten and Kohne (5) proposed a general mechanism for the genesis of all repeated sequences. The creation of a family of clustered repeats—sometimes detected as a density satellite—was envisioned as a salutary event, followed by gradual divergence and dispersal of these family members throughout the genome. But until now, direct interspersion evidence in support of the idea has been lacking. The only previous data consistent with the idea were a low level of hybridization of satellite with main band DNA in the mouse, which was not interpreted as support for interspersion (11) and which later efforts failed to confirm (6). On the basis of our present work, we suggest that in the muskmelon we are witnessing the birth, as a satellite, and initial dissemination of a family of repeated sequences. As the translocation process continues, the satellite in future generations will be converted to a dispersed family of interdispersed repetitive sequences. We anticipate with great interest the further investigation of this single family of dispersed repeated sequences. Such sequences have been thought to function in regulating the expression of genes (4).

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