Resistance in rice to multiplication of the two tungro viruses†
(Kerintangan pokok padi terhadap penggandaan dua virus penyakit merah)


Key words: rice, tungro viruses, multiplication and resistance

Abstrak

Abstract
Multiplication of rice tungro bacilliform virus (RTBV) and rice tungro spherical virus (RTSV) in 14 rice varieties were studied. The sap from each plant was assayed for viral concentration by the enzyme-linked immunosorbent assay (ELISA) at 21 days after seedling inoculation. Mean absorbance or concentration values for RTBV of inoculated plants varied among varieties. The large values in TN1, IR42, MR 106 and MR 81 suggested the high susceptibility of these varieties to RTBV multiplication. The values were intermediate in Latisail, Basmati 370, MR 84, Habiganj DW8 and Y1036 and small in Utri Merah, Utri Rajapan and Balimau Putih. When sap samples of the inoculated Utri Merah and Balimau Putih were assayed at different weeks after inoculation, their ELISA values were consistently small, indicating low RTBV multiplication in the

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varieties. Inoculated plants of Basmati 370, Habiganj DW8, Kataribhog, MR 81, Pankhari 203, Utri Merah, Utri Rajapan and Y1036 gave extremely small mean absorbance values for RTSV, qualitatively uninfected, and failed to serve as inoculum sources, suggesting their resistance to RTSV infection. Balimau Putih which has low multiplication of both RTBV and RTSV is moderately efficient as an inoculum source.

**Introduction**

The green leafhopper (GLH), *Nephotettix virescens* (Homoptera: Cicadellidae), seldom causes direct damage to rice plants (Ling 1972). However, its ability to transmit the tungro agents, rice tungro bacilliform virus (RTBV) and rice tungro spherical virus (RTSV), makes GLH economically important (Hibino et al. 1978; Omura et al. 1983). Rice varieties IR42, Pankhari 203 and Y1036 had resistance to GLH, and these vector resistance contributed in lowering tungro infection rates in these three varieties (Habibuddin et al. 1994). However, vector resistance is easily overcome. Resistant-breaking colonies of GLH increase both RTBV and RTSV infections on IR42, but not RTSV on Pankhari 203 and Y1036 which are resistant to RTSV infection. Hence, such varieties with direct resistance to tungro virus(es) may provide a better alternative in the management of tungro disease. Rice varieties Basmati 370, Habiganj DW8, Kataribhog, MR 81, Utri Merah and Utri Rajapan might also be resistant to RTSV infection (Hibino et al. 1990; Habibuddin et al. 1994).

Plant resistance to a virus can be categorised into five classes, viz. immunity, resistance to virus infection, resistance to virus movement, resistance to virus multiplication and tolerance (Holmes 1965; Bjorling 1966; Russell 1978; Hull 1986; Ponz and Brunning 1986). In the past, plant infection with tungro disease was identified based on its characteristic symptoms. By symptomatology, two categories of resistance can be identified, viz. resistance and tolerance to infection (Ling 1972). Further categorisation requires quantitative analysis of the virus in inoculated plants by various methods, including enzyme-linked immunosorbent assay, ELISA (Clark and Adams 1977). Production of specific antisera to RTBV and RTSV (Omura et al. 1983) has made possible the use of ELISA test for these viruses. ELISA test could be used to detect a low level of RTBV or RTSV in infected rice plant sap (Bajet et al. 1985).

In this study, 14 rice varieties were evaluated for their resistance and tolerance to RTBV and RTSV infection and multiplication by assessing virus concentration and development in inoculated plants and efficiency of tungro-inoculated plants to serve as inoculum source. The generated results may be used to identify promising varieties to be used as resistant sources in the breeding programmes.

**Materials and methods**

**Quantitative virus assay by ELISA**

Susceptibility of 14 rice varieties (*Table 1*) to RTBV and RTSV was assessed by measuring absorbance value in ELISA on tungro-inoculated plants. Three GLH colonies, TN1-colony, IR42-colony or P203-colony (Habibuddin et al. 1994) were used for the inoculation on 10-day-old seedlings of test varieties. Except for IR42, Pankhari 203 and Y1036, seedlings were inoculated using TN1-colony as the vector. IR42 was inoculated using IR42-colony or P203-colony (Habibuddin et al. 1994) were used for the inoculation on 10-day-old seedlings of test varieties. Except for IR42, Pankhari 203 and Y1036, seedlings were inoculated using TN1-colony as the vector. IR42 was inoculated using IR42-colony while Pankhari 203 and Y1036 seedlings were inoculated using P203-colony. Three hills of tungro-(RTBV + RTSV) infected TN1 plants, previously confirmed by the ELISA test, were used as the virus source. The hills were subdivided at the root zone into three portions. Three portions, one from each hill, were combined to form three identical
inoculum sources. GLH adults of the three colonies were allowed 1-day acquisition access feeding on each inoculum source. Ten seedlings of each variety were inoculated individually at 3 GLH/seedling. Three weeks after inoculation (WAI), seedlings were tested in ELISA.

For the ELISA test, the second fully developed leaf from the top was selected (Hibino et al. 1990). Leaf tissue of 0.1 g was homogenised with 1.0 mL of 0.02 M phosphate buffer, pH 7.4. The homogenate of 10x dilution was further diluted with the same buffer to have a series of dilutions (30x, 90x, 270x, 810x and 2 430x). ELISA protocols followed the method of Clark and Adams (1977) using antisera to RTBV and RTSV as described by Omura et al. (1983). Absorbance values at A$_{405}$ for RTBV and RTSV were read using ELISA Reader (SLT LabInstrument, Germany). Virus concentration in the inoculated plants was exhibited by their absorbance values after subtracting the mean absorbance of healthy plant saps. The corrected absorbances above the mean of healthy sap were considered as positively infected. Mean value of corrected absorbance of all inoculated plants was also calculated for each test variety.

Recovery of RTBV and RTSV

The efficiency of tungro-inoculated plants of 14 rice varieties to serve as an inoculum source was compared at 3 WAI. Six virus-inoculated plants of each variety, except IR42, Pankhari 203 and Y1036, were pooled and confined in a cage with 30 adults of the TN1-colony for 1-day acquisition access feeding. For IR42, Pankhari 203 and Y1036, six inoculated plants were separated at their root zone into two portions. Six portions, one from each plant, were pooled and confined with GLH adults of the TN1-colony while the other portions were pooled and confined with their respective adapted colony (IR42-colony or P203-colony).

The GLH were then individually allowed 1-day inoculation access feeding on 7-day-old TN1 seedlings before being given a fatal foliar application of BPMC insecticide (0.1% a.i.). Furadan granule was also given for persistent insect control. Inoculated seedlings were placed in an insect-free compartment for 3 weeks before the ELISA procedure. The experiment was repeated three times. The efficiency of virus recovery by GLH was indicated as percentage GLH that transmitted viruses to TN1 seedlings.

Changes of virus concentration

Changes in virus concentration in tungro-inoculated rice varieties were studied in TN1, Latisail, MR 84, Basmati 370, Utri Merah, MR 81, Balimau Putih and Y1036. These varieties represented the different resistant categories with TN1 serving as the susceptible control. The changes of virus concentration in these varieties were measured using ELISA on the saps of inoculated plants at 2, 4, 6, 8 and 10 WAI.

To serve seedlings at 2, 4, 6, 8 and 10 WAI at once for the quantitative assay, 10 seeds of each variety were soaked consecutively at 2-week intervals. The seeds of each variety were sown in a 25 cm pot. At 7 DAS, seedlings except for Y1036 were inoculated for a day by tungro-viruliferous GLH of the TN1-colony at 3 GLH/seedling. For Y1036, seedlings were inoculated using GLH of the P203-colony. Inoculated seedlings were kept in an insect-free compartment and tested when the first set of seedlings reached 10 WAI. ELISA test was performed in a split plot design with 10 blocks, each corresponded to a microtitre plate. The rows in each microtitre plate represented weeks after inoculation as the main factor while the microwells within rows represented varieties as the subfactor.

Results

Virus concentration in leaves of inoculated plants

There were significant differences among varieties in corrected mean absorbance values for RTBV and RTSV in the ELISA test of leaves from tungro-inoculated plants.
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(\textit{Table 1}). All varieties had corrected mean absorbance values for RTBV larger than that of healthy sap (0.087), indicating that all of them were infected. Corrected mean absorbance value was largest in TN1 (2.631), followed by IR42 and MR 106 in decreasing order. Their relative values to that of TN1 were about 87% and 75% respectively, suggesting their high susceptibility to RTBV infection and multiplication.

MR 81, MR 84, Kataribhog, Latisail, Y1036, Pankhari 203, Basmati 370 and Habiganj DW8 with absorbance values of 30–65% of the TN1 value were moderately susceptible to RTBV multiplication (\textit{Table 1}). Utri Merah, Utri Rajapan and Balimau Putih which exhibited small mean absorbance values, were considered as resistant to the multiplication of RTBV. The mean dilution end point for detection of RTBV was 1/10 in Utri Merah and Utri Rajapan, 1/30 in Balimau Putih, 1/270 in MR 106, and 1/810 in TN1. Corrected mean absorbance value of Utri Merah and Balimau Putih at 1/10 dilution was <0.264, which is smaller than that of TN1 at 1/270 dilution (0.375). This further indicates the low RTBV concentrations in Utri Merah, Utri Rajapan and Balimau Putih.

The corrected mean absorbance values for RTSV similarly showed variations among varieties (\textit{Table 1}). The value was significantly largest in TN1 (1.115), exhibiting its high susceptibility to RTSV multiplication. This was followed in decreasing order by IR42, MR 106 and MR 84, with values ranged from about 72% to 48% that of TN1. Mean absorbance values of Latisail (0.282) and Balimau Putih (0.262) were small but larger than that of healthy leaf sap (0.093), indicating their moderate resistance to RTSV multiplication. The corrected mean absorbance values were not significantly different among Basmati 370, MR 81, Kataribhog, Pankhari 203, Y1036, Habiganj DW8 and Utri Merah, less than the value of healthy plant sap, which

\begin{table}[h]
\centering
\begin{tabular}{lcccccc}
\hline
Variety & \textbf{RTBV} & \multicolumn{2}{c}{\textbf{Mean absorbance$^2$}} & \multicolumn{2}{c}{\textbf{RTSV}} & \\
 & infection (%) & \multicolumn{2}{c}{\textbf{Relative}} & infection (%) & \multicolumn{2}{c}{\textbf{Relative}} \\
 & & \multicolumn{1}{c}{absorbance$^3$} & \multicolumn{1}{c}{absorbance$^3$} & & \multicolumn{1}{c}{absorbance$^2$} & \multicolumn{1}{c}{absorbance$^3$} \\
\hline
Basmati 370 & 100 & 1.044d & 39.7 & 0 & 0.027a & 2.4 \\
Balimau Putih & 90 & 0.387b & 14.7 & 80 & 0.262c & 23.5 \\
Habiganj DW8 & 100 & 0.785c & 29.8 & 0 & 0.008a & 0.7 \\
IR42 & 100 & 2.280h & 86.7 & 100 & 0.800e & 71.7 \\
Kataribhog & 100 & 1.481ef & 56.3 & 20 & 0.067abc & 6.0 \\
Latisail & 100 & 1.363e & 51.8 & 70 & 0.282c & 25.3 \\
MR 81 & 100 & 1.679f & 63.8 & 20 & 0.077abc & 6.9 \\
MR 84 & 100 & 1.698f & 64.5 & 100 & 0.531d & 47.7 \\
MR 106 & 100 & 1.976g & 75.1 & 100 & 0.620d & 55.6 \\
Pankhari 203 & 100 & 1.274de & 48.4 & 20 & 0.055ab & 5.0 \\
Utri Merah & 90 & 0.201ab & 7.6 & 20 & 0.032a & 2.9 \\
Utri Rajapan & 60 & 0.115a & 4.4 & 80 & 0.171bc & 15.4 \\
Y1036 & 100 & 1.630f & 62.0 & 10 & 0.090ab & 8.0 \\
TN1 & 100 & 2.631i & 100.0 & 100 & 1.115f & 100.0 \\
Healthy sap & (0.087) & - & (0.093) & - & - & - \\
\hline
\end{tabular}
\caption{Mean absorbance values for RTBV and RTSV in ELISA of tungro-inoculated plants of 14 rice varieties$^1$}
\end{table}

$^1$Absorbance of 10x sap of the second fully developed leaf from the top
$^2$Values are corrected absorbance after substracting the original values with the mean absorbance of healthy sap. Values larger than that of the healthy sap are considered positively infected. All mean values in each column with a common letter are not significantly different at $p = 0.05$ level by DMRT
$^3$Relative to the TN1 value
suggest the low or absence of RTSV infection in the varieties (Table 1). Utri Rajapan had a slightly larger mean absorbance value (0.171) because >80% of its inoculated seedlings were qualitatively infected, albeit their absorbance values were small (<2x of healthy sap). Mean dilution end point for RTSV of TN1 was 1/270. Mean ELISA value of TN1 at 1/90 dilution was 0.492 which was significantly larger than the values of Utri Merah, Basmati 370, Kataribhog, Pankhari 203, Y1036 or Habiganj DW8 at 1/10 dilution.

Recovery of RTBV and RTSV

Percentage of GLH that recovered RTBV and RTSV in combination from RTBV + RTSV-inoculated plants was larger for MR 106 (98.9%) and TN1 (80.0%), suggesting their high efficiency to serve as an inoculum source (Table 2). These were followed in decreasing order by MR 84, Balimau Putih and IR42. Percentage of GLH recovered RTBV + RTSV was small from Latisail (14.4%) and nil from Basmati 370, Habiganj DW8, Kataribhog, MR 81, Pankhari 203, Utri Merah, Utri Rajapan and Y1036. Percentage of GLH that recovered RTBV + RTSV seemed to be correlated with the mean absorbance values in ELISA for RTBV ($r = 0.5112^{*}$) and RTSV ($r = 0.8088^{***}$).

Some GLH used in the recovering test transmitted only RTBV from tungro-inoculated plants of several varieties (Table 2). For all varieties except Latisail, less GLH transmitted only RTBV than those that transmitted RTBV + RTSV. For tungro-inoculated Latisail plants, there was 43.42% of RTBV-alone transmitters compared with 14.4% RTBV + RTSV transmitters. None of the GLH used transmitted either viruses.

### Table 2. Mean absorbance values in ELISA of tungro-inoculated plants of 14 varieties and virus recovery from inoculated plants

<table>
<thead>
<tr>
<th>Source of inoculum (variety)</th>
<th>Mean absorbance of source plant</th>
<th>Percentage GLH that recovered viruses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>RTBV</td>
<td>RTSV</td>
</tr>
<tr>
<td>Basmati 370</td>
<td>0.963</td>
<td>0.024</td>
</tr>
<tr>
<td>Balimau Putih</td>
<td>0.426</td>
<td>0.261</td>
</tr>
<tr>
<td>Habiganj DW8</td>
<td>0.840</td>
<td>0.002</td>
</tr>
<tr>
<td>IR42</td>
<td>2.339</td>
<td>0.863</td>
</tr>
<tr>
<td>IR42³</td>
<td>2.339</td>
<td>0.863</td>
</tr>
<tr>
<td>Kataribhog</td>
<td>1.442</td>
<td>0.055</td>
</tr>
<tr>
<td>Latisail</td>
<td>1.299</td>
<td>0.224</td>
</tr>
<tr>
<td>MR 81</td>
<td>1.583</td>
<td>0.067</td>
</tr>
<tr>
<td>MR 84</td>
<td>1.551</td>
<td>0.539</td>
</tr>
<tr>
<td>MR 106</td>
<td>1.951</td>
<td>0.583</td>
</tr>
<tr>
<td>Pankhari 203</td>
<td>1.167</td>
<td>0.050</td>
</tr>
<tr>
<td>Pankhari 203 ³</td>
<td>1.167</td>
<td>0.050</td>
</tr>
<tr>
<td>Utri Merah</td>
<td>0.184</td>
<td>0.002</td>
</tr>
<tr>
<td>Utri Rajapan</td>
<td>0.058</td>
<td>0.147</td>
</tr>
<tr>
<td>Y1036</td>
<td>1.756</td>
<td>0.106</td>
</tr>
<tr>
<td>Y1036 ³</td>
<td>1.756</td>
<td>0.106</td>
</tr>
<tr>
<td>TN1</td>
<td>2.695</td>
<td>1.172</td>
</tr>
<tr>
<td>Control</td>
<td>0.087</td>
<td>0.093</td>
</tr>
</tbody>
</table>

1 Mean values from six replicates
2 Mean values from 30 seedlings/replicate and three replications/source variety. All mean values in each column with a common letter are not significantly different at $p = 0.05$ level by DMRT
3 IR42-colony was used for the recovery
4 P203-colony was used for the recovery
from tungro-inoculated plants of Basmati 370, Habiganj DW8, Kataribhog, MR 81, Pankhari 203, Utri Merah, Utri Rajapan or Y1036.

GLH of the TN1-colony that recovered RTBV + RTSV as well as RTBV and RTSV separately from tungro-inoculated IR42 plants was 33.3, 21.1 and 1.1%, respectively. In comparison, GLH of the IR42-colony recovered the viruses from the same source plants was 46.7, 28.9, and 4.8%, respectively (Table 2). The results showed that the IR42-colony dispersed RTBV and RTSV from tungro-inoculated IR42 plants better than the TN1-colony. However, P203-colony as well as TN1-colony failed to recover either viruses from tungro-inoculated Pankhari 203 or Y1036 plants.

**Changes of virus concentration**

Analysis of variance indicated that varietal component was the most predominant factor (79%) affecting variations in mean absorbance for RTBV in ELISA of leaves from tungro-inoculated plants, while the time or weeks after inoculation (WAI) and interaction between the two factors contributed about 3 and 2%, respectively. Irrespective of WAI, the mean absorbance values were large in TN1 and MR 81, intermediate in MR 84, Latisail, Basmati 370 and Y1036, and small in Utri Merah and Balimau Putih. The mean absorbance values, however, were all larger than the value of healthy sap. Except for MR 84, Latisail and Basmati 370, mean absorbance values did not change remarkably with the progress of time after inoculation (Figure 1). In MR 84, Latisail and Basmati 370, the absorbance for RTBV was slightly reduced with progress of time as indicated by the presence of significant negative correlation (r) and regression coefficient (b) values among the varieties.

Similarly, varietal component (84%) was also the predominant factor influencing the mean absorbance values for RTSV. Generally, the mean absorbance value was largest in TN1, followed in decreasing order by Latisail, MR 84 and Balimau Putih. In each variety, differences in the values at different WAI were small. The mean absorbance values in Utri Merah, Y1036, Basmati 370 and MR 81 were smaller than that of the healthy sap, indicating their resistance to RTSV infection or multiplication. Except for Latisail, mean absorbance readings for RTSV of most varieties did not change remarkably with time after inoculation (Figure 2). In Latisail, the absorbance was reduced (r = −0.682**) with the progress of infection.

**Discussion**

In the ELISA test, the absorbance values for virus antigen are proportional to the concentration of the virus in the test plant saps (Clark and Adams 1977). Based on this assumption, virus-infected plant tissues which give a larger absorbance reading in ELISA, may have more virus, and thus the plant is more susceptible to virus multiplication, while plant tissues giving a small reading have less virus in the plant and the plant is more resistant to its multiplication. In this study, the quantitative tests of virus-infected sap showed differences in the absorbance values for either RTBV or RTSV among the test varieties. These differences suggested variations in the levels of resistance to virus infection and/or virus multiplication among the varieties.

The concentration of RTBV was high in TN1, IR42, MR 106 and MR 81, and intermediate in Latisail, Basmati 370, MR 84, Habiganj DW8 and Y1036. This classification, as based on ELISA values, might not be accurate in describing the actual presence of infectious virus particles in the inoculated plants since the assay also detected coat protein aggregates and non-infectious virus particles present in the sap. However, Dahal et al. (1992) showed a high correlation between coat protein by ELISA and viral nucleic acid by DNA hybridisation. Hence, ELISA values may
provide a relative virus concentration in the tested sap. Takahashi et al. (1993) demonstrated the low concentration of RTBV virus in RTBV-infected leaf tissues of Utri Merah, Utri Rajapan and Balimau Putih by both the ELISA and polymerase chain reaction (PCR) technique. In this study, Utri Merah, Utri Rajapan and Balimau Putih also showed relatively low RTBV concentration in the inoculated leaves even at several weeks after inoculation. Utri Merah was previously classified as resistant to RTBV multiplication (ShahJahan et al. 1990). The present data revealed that Utri Rajapan and Balimau Putih may also be resistant to RTBV multiplication. Sta Cruz et al. (1993) suggested that the low concentration of RTBV in Balimau Putih and Utri Merah was attributed to the fewer susceptible cells present in the varieties besides low multiplication of the virus within their cells.

Similarly, large absorbance values in ELISA for RTSV in TN1, IR42, MR 106 and MR 84 indicated high RTSV concentration and their susceptibility to its multiplication. Intermediate concentration in Latisail and Balimau Putih demonstrated their moderate resistance to RTSV multiplication. Extremely small absorbance values in Basmati 370, Habiganj DW8, Kataribhog, MR 81, Pankhari 203, Utri Merah and Y1036, even when tested at 2–10 WAI, is a further indication of their
resistant in rice to multiplication of tungro viruses

Figure 2. Changes in mean absorbance values of ELISA for RTSV of tungro-inoculated plants of eight rice varieties determined at 2–10 weeks after the inoculation

<table>
<thead>
<tr>
<th>Variety</th>
<th>Linear regression</th>
<th>Correlation coefficient (r)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>b1</td>
<td>SE</td>
</tr>
<tr>
<td>Balimau Putih</td>
<td>0.009ns</td>
<td>0.012</td>
</tr>
<tr>
<td>Basmati 370</td>
<td>-0.004ns</td>
<td>0.001</td>
</tr>
<tr>
<td>Latisail</td>
<td>-0.042***</td>
<td>0.006</td>
</tr>
<tr>
<td>MR 81</td>
<td>0.004ns</td>
<td>0.002</td>
</tr>
<tr>
<td>MR 84</td>
<td>0.003ns</td>
<td>0.010</td>
</tr>
<tr>
<td>Utri Merah</td>
<td>-0.002ns</td>
<td>0.002</td>
</tr>
<tr>
<td>Y1036</td>
<td>-0.004ns</td>
<td>0.003</td>
</tr>
<tr>
<td>TN1</td>
<td>-0.013ns</td>
<td>0.010</td>
</tr>
</tbody>
</table>

*significant at p = 0.05 level  **significant at p = 0.01 level  ***significant at p = 0.001 level

Varieties such as Kataribhog, Pankhari 203 and Utri Rajapan showed the presence of a few infected seedlings (Table 1) as previously observed elsewhere (Hibino et al. 1990), albeit their corrected ELISA values which were extremely small. Probably these small absorbance values were due to false positive values (Sutula et al. 1986).

Varieties like Basmati 370, Habiganj DW8, Kataribhog, MR 81, Pankhari 203, Utri Merah, Utri Rajapan and Y1036 also failed to become effective sources of RTSV infection. Should Basmati 370 and other varieties be positively infected with RTSV, then the ‘helper factor’ in the RTSV-infected plants would help in GLH transmission of RTBV (Hibino 1983), as RTBV concentration in these varieties was relatively high. Previously, Hibino et al. (1979) showed that RTSV particles were transmitted by GLH either from plants infected singly with RTSV or doubly with RTBV + RTSV. This study demonstrates that RTSV is not transmitted from these tungro-inoculated plants, reflecting the low or absence of RTSV infection among plants of these varieties, a further evidence of their resistance to RTSV infection.

The efficiency of tungro-inoculated plants to serve as an inoculum source was positively correlated with the concentration of RTBV ($r = 0.5112^*$) and RTSV ($r = 0.8088^{**}$). Percentage of GLH
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recovered RTBV and/or RTSV from tungro-inoculated plants was higher in TN1 and MR 106 than that in Balimau Putih, a moderately resistant variety to the multiplication of both RTBV and RTSV. The influence of virus concentration on viral transmission efficiency has previously been reported (Aiyanathan and Narayanasamy 1989; Pereira and Lister 1989). The results obtained in this study also demonstrated that GLH transmission efficiency from vector-resistant varieties such as IR42 was higher when its resistant-breaking colony was used as the vector.

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References


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