GENETIC STUDIES ON COOL TOLERANCE IN RICE

IV. Direct and Indirect Effects of Selection for Cool Tolerance

YUZO FUTSUHARA* and Kunio TORIYAMA**

* Faculty of Agriculture, Nagoya University, Nagoya 464
** Chugoku Agricultural Experiment Station, Fukuyama 720

Synopsis. Selections for cool tolerance were practised in F₃ under two different selection intensities, and their effects were evaluated in F₄ generation. It was found that through the selection for cool tolerance, the noticeable genetic shifts were produced not only for cool tolerance, but also for several characters such as culm length, ear length and number of ears to which selections were not applied. As for these characters, in general, there was observed close agreement between the expected and observed responses of the F₃ population to selection.

Introduction

In the second report of the present series, it was reported that there was a negative genetic correlation between cool tolerance (expressed by sterility index) and culm length, regardless of the plant types of the parental varieties, in the crosses of Somewake × Aomori No. 5 and Kitakei No. 3204 × Ōu No. 187. This result demonstrates that in the segregating population, the selections for cool tolerance would produce a pronounced genetic shift in some characters correlated with cool tolerance, bringing about a considerable difficulty on the breeding of cool-tolerant varieties with high productivity.

According to Falconer (1964), the genetic shift in a character correlated with a character to which selection was applied can be predicted if the genetic correlation coefficient and heritabilities of the two characters are known. Conversely, if the correlated response is measured by selection experiment, thereby the accuracy of heritabilities and genetic correlation can be evaluated.

The present study was an attempt to obtain information on the response of hybrid population in cool tolerance on which character selection was applied on F₃ line basis (direct response) and on the responses in other characters which were not subjected to selection ( indirect response).

Materials and Methods

The F₁~F₄, B₁ and B₂ of the cross of Somewake and Aomori No. 5 were used in this study. Details about these materials have already been described in the paper by Toriyama and Futsuhara (1960).

Records were taken on cool tolerance, culm length, ear length, number of ears, number of grains per ear and heading date. Cool tolerance was evaluated by sterility of the materials tested in the field irrigated moderately with cool water. The sterility percentage was rescaled by the inverse sine transformation in calculating genetic parameters. According to Mather’s method (1949), total variation in each character measured was partitioned into D, H and E components. Based on these estimates, heritability of each character for F₃ line was calculated as,

\[ h^{2}_{F₃} = \frac{1}{\frac{1}{2}D + \frac{1}{16}H + E₄} \]  \hspace{1cm} (1)

and genetic correlation was calculated as,

\[ r_{XY} = \frac{Cov_{XY}}{\sqrt{V_{XX}V_{YY}}} \]  \hspace{1cm} (2)

where Cov_{XY} stands for the genetic covariance of characters X and Y, and V_{XX} and V_{YY} stand for the genetic variances of characters X and Y, respectively. According to Lerner’s method (1958), the genetic gain of the character X directly subjected to selection was calculated as,
\[ \Delta G = i_x h_x \sigma_{Gx}, \quad (3) \]

where \( i_x \), \( \sigma_{Gx} \) and \( h_x \) stand for the standardized selection differential, genetic standard deviation and square root of heritability for character \( X \), respectively.

The consequent change of a character \( Y \) to selection applied to character \( X \), is therefore given as,

\[ \Delta G = b_{xy} \Delta G, \quad (4) \]

where \( b_{xy} \) stands for the regression of the genetic gain of \( Y \) on the genetic gain of \( X \).

Or, by putting

\[ b_{xy} = \frac{\text{Cov}\{G_x, G_y\}}{\sigma_{Gx}^2}, \text{ and } \sigma_{Gy} = h_y \sigma_{Gy}, \]

the correlated response can be rewritten as,

\[ \Delta G = \frac{\sigma_{Gy}}{\sigma_{Gx}} \Delta G_x \]
\[ = \frac{i_x h_x}{i_x h_y} \sigma_{Gy} \]
\[ = i_x h_x h_y \sigma_{Gy}, \quad (5) \]

The following diagram represents the genetic relationship between characters \( X \) and \( Y \),

\[ X \xrightarrow{h_x} G_x \xrightarrow{\sigma_{Gx}} Y \xrightarrow{h_y} G_y \]

Meanwhile, selections for cool tolerance were practised on \( F_3 \) and their effects were evaluated in \( F_4 \) in the following ways: the five highest, ten highest, five lowest and ten lowest lines for cool tolerance were selected from the original 50 \( F_4 \) lines which were grown in the field under cool water irrigation, and progenies of these selected lines, each containing two lines were compared with the 50 unselected families.

### Results

1. **Heritability and genetic correlation**

The values of the D, H and E components in each character estimated according to MATHER’s method are shown in Table 1. In general, the additive genetic component D was considerably larger than the environmental component E. In all characters except number of ears, the nonadditive genetic component H were negative values. However, these values could generally be considered of nonsignificance when their large standard error values (\( s_H \)) were taken into account.

The heritabilities and genetic correlations for \( F_3 \) lines computed from the estimates of the above components are shown in Table 2. The heritabilities for various agronomic characters were considerably higher than those reported by other workers (WEBER and MOORHY, 1952; JOHNSON et al., 1955; AXEMINE and KUMAGAI, 1958). This can probably be explained by the relatively small environ-

### Table 1. Estimates of variance components for main characters

<table>
<thead>
<tr>
<th>Item</th>
<th>Variance component</th>
<th>Cool tolerance Observed</th>
<th>Culum length Observed</th>
<th>Ear length Observed</th>
<th>No. of ears per ear Observed</th>
<th>No. of grains per ear Observed</th>
<th>Heading date Observed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Observed</td>
<td>Expected</td>
<td>Observed</td>
<td>Expected</td>
<td>Expected</td>
<td>Expected</td>
</tr>
<tr>
<td>( V_{F1} )</td>
<td>( 1/2 ) ( D + 1/2 ) H + E1</td>
<td>174.3436 183.7020</td>
<td>21.7453 22.7311</td>
<td>1.3405</td>
<td>1.4320</td>
<td>0.3852</td>
<td>14.7021</td>
</tr>
<tr>
<td>( V_{F2} )</td>
<td>( 1/2 ) ( D + 1/2 ) H + E2</td>
<td>150.2145 140.6661</td>
<td>17.6828 21.0911</td>
<td>1.0496</td>
<td>0.8946</td>
<td>7.9852</td>
<td>6.7605</td>
</tr>
<tr>
<td>( \bar{V}_{F2} )</td>
<td>( 1/4 ) ( D + 1/4 ) H + E1</td>
<td>86.1213 94.9123</td>
<td>22.8204 21.1581</td>
<td>1.4311</td>
<td>1.3608</td>
<td>6.0129</td>
<td>8.6269</td>
</tr>
<tr>
<td>( V_{F_{26}} )</td>
<td>( 1/2 ) ( D + 1/2 ) H + E2</td>
<td>125.2910 126.2951</td>
<td>27.4450 20.9819</td>
<td>0.8905</td>
<td>0.8728</td>
<td>5.1720</td>
<td>4.4476</td>
</tr>
<tr>
<td>( W_{F1}+F_{26} )</td>
<td>( 1/2 ) ( D + 1/2 ) H</td>
<td>122.1969 122.8310</td>
<td>14.8268 18.2204</td>
<td>0.6065</td>
<td>0.7130</td>
<td>4.3072</td>
<td>3.1659</td>
</tr>
<tr>
<td>( V_{B1}+V_{B2} )</td>
<td>( 1/2 ) ( D + 1/2 ) H + 2E1</td>
<td>255.7164 249.9790</td>
<td>25.4353 25.9168</td>
<td>2.1548</td>
<td>2.1314</td>
<td>29.3248</td>
<td>26.7566</td>
</tr>
<tr>
<td>Nonheritable component</td>
<td>( E_1 )</td>
<td>20.9252 20.5060</td>
<td>13.7474 12.7997</td>
<td>0.9149</td>
<td>0.8596</td>
<td>7.0847</td>
<td>7.9085</td>
</tr>
<tr>
<td></td>
<td>( E_2 )</td>
<td>5.1835 12.3311</td>
<td>4.3667 4.1969</td>
<td>0.2022</td>
<td>0.2861</td>
<td>1.5312</td>
<td>3.0817</td>
</tr>
<tr>
<td></td>
<td>( E_3 )</td>
<td>23.3779 14.5868</td>
<td>15.0399 16.6808</td>
<td>1.0996</td>
<td>1.0791</td>
<td>7.8438</td>
<td>5.2300</td>
</tr>
</tbody>
</table>

Estimates of each component

\[ \begin{align*}
D & = 234.8566 \pm 15.7647 \\
H & = 172.8934 \pm 50.6538 \\
E_1 & = 23.0506 \pm 10.0630 \\
E_2 & = 12.3311 \pm 8.4713 \\
E_3 & = 14.5868 \pm 8.0254 \\
\end{align*} \]

\[ \text{Note: } E_1 = \frac{V_{F2} + V_{F1}}{2}, \quad E_2 = \frac{V_{F2} + V_{F2}}{2}, \quad E_3 = \frac{V_{F2} + V_{F3} + V_{F2} + V_{F2}}{2} \]

\[ n: \text{Number of plants, } l: \text{Number of lines} \]

\[ *: \text{The results of the previous report (1969).} \]
mental variance in comparison to the large
total variances due to the extreme genetical
remoteness of the cross parents. The magni-
tude of the heritability was in the following
order: culm length > heading date > cool
tolerance > ear length > number of grains per
ear > number of ears, being in accord with the
results obtained by other workers. Cool
tolerance was closely correlated with culm
length, ear length, number of ears and number
of grains per ear but was little related with
heading date.

2. Selection differential

The means of main characters of the F₃
lines selected for high or low cool toler-
ance and unselected lines are shown in Table 3.
The standardised selection differentials which
were estimated from the values in Table 3
are given in Table 4.

In general, the lines selected for high cool
tolerance showed marked increase in culm
length, ear length and number of ears, but
decrease in number of ears, while the selec-
tions for low cool tolerance showed responses
with the almost identical magnitude but with
opposite sign in the most characters. In other
words, the selections for high and low cool
tolerance produced the pronounced shifts of
F₃ lines toward Somewake or Aomori No. 5
type with respect to these characters.

On the other hand, in spite of the fact
that both the parents were intermediate in
maturity, their F₃ population had a considerable
variability in heading date, and both the

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Table 2. Genetic correlations and heritabilities of main characters for F₃ lines

<table>
<thead>
<tr>
<th>Character</th>
<th>Cool tolerance</th>
<th>Culm length</th>
<th>Ear length</th>
<th>No. of ears</th>
<th>No. of grains per ear</th>
<th>Heading date</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cool tolerance</td>
<td>-0.4760</td>
<td>0.7052</td>
<td>0.3648</td>
<td>-0.3904</td>
<td>19.1494</td>
<td>3.3183</td>
<td>0.8935</td>
</tr>
<tr>
<td>Culm length</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.9271</td>
</tr>
<tr>
<td>Ear length</td>
<td>-0.4853</td>
<td></td>
<td></td>
<td>0.5815</td>
<td>19.1494</td>
<td>3.3183</td>
<td>0.9271</td>
</tr>
<tr>
<td>No. of ears</td>
<td>-0.4281</td>
<td></td>
<td></td>
<td>-0.4091</td>
<td>19.1494</td>
<td>3.3183</td>
<td>0.9271</td>
</tr>
<tr>
<td>No. of grains per ear</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.9271</td>
</tr>
<tr>
<td>Heading date</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.9271</td>
</tr>
<tr>
<td>Phenotypic σ</td>
<td>12.2562</td>
<td>4.2049</td>
<td>1.0245</td>
<td>2.8223</td>
<td>19.1494</td>
<td>3.3183</td>
<td>0.9271</td>
</tr>
</tbody>
</table>

Table 3. Means of main characters in F₃ lines selected for cool tolerance

<table>
<thead>
<tr>
<th>Percentage of F₃ saved</th>
<th>Cool tolerance</th>
<th>Culm length</th>
<th>Ear length</th>
<th>No. of ears</th>
<th>No. of grains per ear</th>
<th>Heading date</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>sin⁻¹√%</td>
<td>cm</td>
<td>cm</td>
<td></td>
<td></td>
<td>day/Aug.</td>
</tr>
<tr>
<td>lower 10</td>
<td>69.760</td>
<td>80.240</td>
<td>15.060</td>
<td>14.180</td>
<td>91.700</td>
<td>14.700</td>
</tr>
<tr>
<td>lower 20</td>
<td>63.970</td>
<td>80.070</td>
<td>15.330</td>
<td>12.660</td>
<td>97.580</td>
<td>14.480</td>
</tr>
<tr>
<td>unselected</td>
<td>43.822</td>
<td>82.750</td>
<td>16.340</td>
<td>11.470</td>
<td>111.984</td>
<td>13.346</td>
</tr>
<tr>
<td>Somewake (P₁)</td>
<td>27.223</td>
<td>90.168</td>
<td>17.536</td>
<td>8.661</td>
<td>145.532</td>
<td>13.132</td>
</tr>
<tr>
<td>Aomori No. 5 (P₂)</td>
<td>84.852</td>
<td>72.303</td>
<td>14.852</td>
<td>20.352</td>
<td>73.439</td>
<td>13.381</td>
</tr>
</tbody>
</table>

Table 4. Standardised selection differentials by F₃ line selection for cool tolerance

<table>
<thead>
<tr>
<th>Percentage of F₃ saved</th>
<th>Cool tolerance</th>
<th>Culm length</th>
<th>Ear length</th>
<th>No. of ears</th>
<th>No. of grains per ear</th>
<th>Heading date</th>
</tr>
</thead>
<tbody>
<tr>
<td>upper 10</td>
<td>-1.420</td>
<td>0.667</td>
<td>0.547</td>
<td>-0.188</td>
<td>-0.216</td>
<td>0.420</td>
</tr>
<tr>
<td>upper 20</td>
<td>-1.182</td>
<td>0.391</td>
<td>0.381</td>
<td>-0.429</td>
<td>-0.025</td>
<td>0.420</td>
</tr>
<tr>
<td>lower 10</td>
<td>2.116</td>
<td>-0.598</td>
<td>-1.249</td>
<td>0.960</td>
<td>-0.986</td>
<td>0.408</td>
</tr>
<tr>
<td>lower 20</td>
<td>1.644</td>
<td>-0.639</td>
<td>-0.986</td>
<td>0.422</td>
<td>-0.752</td>
<td>0.342</td>
</tr>
</tbody>
</table>
1. Cool tolerance

2. Culm length

3. Ear length

4. Number of ears

5. Number of grains per ear

6. Heading date

Note:
- : F₄ distribution
- : F₄ progenies derived from the upper or lower five F₃ lines for cool tolerance
- : F₄ progenies derived from the next upper or lower five F₃ lines for cool tolerance

ΔG₁, ΔG₄: Genetic gain by upward selection (a) with selection intensity of 10 or 20%, respectively.
ΔG₂, ΔG₃: Genetic gain by downward selection (b) with selection intensity of 10 or 20%, respectively.

Fig. 1. Frequency distributions of main characters in F₄ progenies derived from selected and unselected F₃ lines for cool tolerance.
lines selected for high and low cool tolerance tended to deviate somewhat toward late ear emergence.

3. Direct and indirect effects of F<sub>4</sub> line selection for cool tolerance

As shown in Fig. 1, remarkable responses in cool tolerance to two way selections for this character on F<sub>4</sub> line basis were observed in F<sub>4</sub> families, although responses to both the selections slackened off somewhat toward high cool tolerance. The F<sub>4</sub> line selection for cool tolerance was considered to be effective even when selection was perfomed moderately.

Furthermore, it can be seen from Fig. 1 that the selection pressure applied toward high cool tolerance might bring about increase in culm length and ear length and decrease in number of ears. In general, the magnitudes of the responses in other characters which were not subjected to selection were greater in the stringent selections than in the moderate selections. These results suggest that the extreme selection for cool tolerance would increase the probability of missing short culm or tillering types. Likewise, the selections for low cool tolerance had influence on these characters. On the other hand, neither of the two way selections had, generally, influence on heading date and number of grains per ear.

Subsequently, the standardised magnitudes of the direct and indirect responses to the F<sub>4</sub> line selection for cool tolerance were estimated according to Lerner's method and compared with the observed ones in F<sub>4</sub> families. These results are given in Table 5. In all selection methods, the agreement between the expected and observed direct responses was good, although the former value was somewhat higher than the latter one. Comparison of the expected indirect responses with the observed ones showed that they were in fairly good agreement, although there were discrepancies in some characters, particularly number of ears and heading date.

**Discussion**

It would be advantageous to plant breeders if the heritabilities and genetic correlations could accurately be estimated. However, it must be kept in mind that the data obtained on any one material or at any one location can not be considered as adequate information for the practical selection. In addition, the different methods for calculating the heritabilities and genetic correlations do not necessarily give the same results. According to Frey and Horner (1955), the usefulness of heritability percentages depends upon their reliability which in turn can be proved only in practice. Also, Clayton et al. (1956) reported that the most accurate genetic correlation was obtained by observation of the response in one character on selection for the other. So the present study was conducted to examine the accuracy of the heritabilities and genetic correlations by comparing the expected gains with those actually obtained in the selection experiments. Hereupon, in the case where the expected values are larger than the observed ones, this discrepancy may
be generally attributed to the following two factors: (1) the heritabilities and/or genetic correlations are overestimated, (2) the forces controlling the preservation of phenotypic balance between components of fitness in order to obviate an extraordinary shift of any character might operate. On the contrary, in the case where the expected values are smaller than the observed ones, the discrepancies may be attributed to the underestimations of heritabilities and/or genetic correlations.

The results obtained herein showed that the agreements between the expected values and observed ones were good in cool tolerance, directly subjected to selection, and in culm length, and ear length which were closely correlated with cool tolerance, although the expected values for the former were slightly larger than the observed ones, whilst the expected values for the latter two were somewhat smaller than the corresponding observed ones. This results indicate that the values of heritabilities and genetic correlations estimated in this study were realistic and reliable, and that it might be possible to predict how much direct and indirect responses would be produced as a result of selection for cool tolerance, by using the heritability and genetic correlation, in so far as the above mentioned characters were concerned. On the other hand, the expected gains for number of ears, number of grains per ear and heading date were somewhat erratic and generally in rather poor agreement with the observed ones, mainly because of their small genetic correlation with cool tolerance.

From the practical point of view, it should be noticed that through the intensive selection for cool tolerance, the noticeable genetic gains were obtained not only for cool tolerance, directly subjected to selection, but also for several characters such as culm length, ear length and number of ears which were not directly subjected to selection, suggesting that there would be considerably large barrier to the breeding of cool-tolerant varieties with high productivity. When the magnitudes of the indirect responses to the moderate selection for cool tolerance are considered, however, this barrier seemed to be neither inevitable nor fatal. It could be expected that the continious moderate selection for cool tolerance would be superior to the extreme one in the early segregating generations, although the definite conclusion must await the detailed studies on the effect of the continious selection for cool tolerance.

**Summary**

The present study was conducted to evaluate the direct and indirect effects of F3 line selection for cool tolerance by using the rice hybrids derived from the cross of Somewake × Aomori No. 5.

As the results, remarkable responses in cool tolerance to two way selections for this character on F3 line basis were observed in F4 families, indicating that the selection for cool tolerance would be feasible in early segregating generations. In addition, as the selection intensity increased for cool tolerance, correlated positive responses were observed for culm length and ear length, and negative responses for number of ears.

When the expected gains estimated from the method of variance component analysis were compared with the observed ones obtained through the selection experiments, the agreements were fairly good regarding to cool tolerance, culm length and ear length.

**Acknowledgment**

The authors wish to thank Professor T. Matsuo and Dr. S. Iyama for their valuable advice and suggestions.

**Literature Cited**


水稲における耐冷性の遺伝と選抜に関する研究

IV. 耐冷性に関するF3系統選抜の直接効果および間接的作

粟原 雄三・鳥山 国士
（名古屋大学農学部）（中国農業試験場）

水稲品種組合せ、染分×青森5号を供試して、耐冷性に関するF3系統選抜の効果について検討した。耐冷性の選抜は、弱2方向へそれぞれ選抜率10%および20%の強さをもって行なったが、選抜の効果はいずれの場合にも顕著に認められた。一方、選抜の間接的的作用として、耐冷性強方向への選抜においては、長さ、大穂、少げつ型、すなわち、染分型への偏りがみられ、弱方向への選抜においては、短穂、小穂、多げつ型、すなわち、青森5号型への偏りが認められた。とくに、強い耐冷性の選抜を行なった場合に顕著な偏りが認められたこと

このような耐冷性の選抜の直接効果および間接的にみられる効果について、期待値をLERNERの方法によって推定し、実測値と比較した結果、直接選抜の対象となった耐冷性、およびそれに遺伝相関の高い稈長、穂長につれは両者かなりよく一致した。したかつて、本研究で推定したこれらの形質に関する遺伝力および遺伝相関値は一応実用的に信頼しうる値と考えられ、またこれらの遺伝相関を用いて、耐冷性の選抜による直接効果および間接的作用を推定することはほぼ可能といえよう。一方、環境変動が大きく、あるいは間接的的作用の小さい数、1穂粒数および出穗期については、期待値と実測値との適合度は低かった。