Short Communication

Diallel Analysis of Leaf Traits in Rice

Masayuki Muraï¹, Toshiro Kinoshita⁰ and Shohei Hirose¹

¹ College of Agriculture and Veterinary Medicine, Nihon University,
Setagaya-ku, Tokyo, ☑ 154
² Plant Breeding Institute, Faculty of Agriculture, Hokkaido University,
Sapporo, ☑ 060

Leaf morphological characters were investigated with the diallel analysis by using
F₁'s among the five Hokkaido varieties. The additive gene effects predominated over
the dominance effects in all characters. h (the total sum of the dominances of the
loci) was significantly positive in the lengths of the second and third leaves, but was
negative in the first leaf width. Two or more genes may affect to each character,
as estimated with the one formula, (the maximum parent value - the minimum parent
value)/2D. Correlation coefficients among the characters indicated a trend that a short
culm genotype had short, narrow and erect leaves, and vice versa.

KEY WORS: Oryza sativa L., rice, diallel analysis, hybrid, dominance, plant type,
leaf angle.

Introduction

Leaf characters in rice, e.g. length and angle were initially measured and regarded as
important by Tsunoda (1959a,b) for examining structures of photosynthetic production,
and studies of Tanaka et al. (1964, 1966, 1968) and many others supported it. Although
varietal differences as to such characters were generally recognized, genetic studies were
few.

We previously carried out the diallel analysis of characters directly related to yield
(Muraï et al., 1986). In this paper, we report the results on some leaf morphological
characters analyzed by the same materials and methods as in the previous paper (Muraï
et al., 1986). Further, correlations among these characters and culm length are investi-
gated. Pleiotropic effects of the genes concerned are discussed.

Materials and Methods

The five varieties of Hokkaido, the northern region of Japan, were used as parents.
They have significantly different leaf characters, as shown in Table 1. Narukaze has the
shortest and erectest leaves, while Ishikarishiroke has the longest and droopiest ones.
The parents and their ten F₁ hybrids without reciprocals were grown in the paddy field
after transplanting with single plant per hill. The randomized block design with two
replicates was applied. The details of the cultivation were described in the previous paper
(Muraï et al., 1986). At maturity, the angle between the basal part of the first (flag)
leaf and the uppermost part of the main culm was measured for six plants per plot in
the field. The lengths of the uppermost three leaf blades and culm, and the width of
the first leaf were measured for the plants after sampled and air-dried.

Received December 17, 1986.
Diallel analysis was carried out on these leaf characters, based on Hayman (1954 a, b) and Jones (1965).

Results and Discussion

The figures of the observed characters of the parents and their F₁'s are presented in Table 1. The analysis of variance was carried out (Table 2). The a and b items in Table 2 indicate the mean square due to the additive effects of the genes and that due to the dominances of some of the loci, respectively. The a item was remarkably larger than the b item for all characters, suggesting that the additive effects predominated over the dominance effects.

In order to ascertain that each character satisfied the six hypotheses for the diallel analysis assumed by Hayman (1954 b), i.e. "Independent action of non-allelic genes", etc., the heterogeneity of Wᵥ₋Vᵥ, and the regression coefficient of Wᵥ on Vᵥ were tested. Variations of five characters except the first leaf length satisfied the hypotheses at the 0.05 probability level or less (the table was abridged).

For the five characters which satisfied the hypotheses, analyses by using the components of variation were carried out (Table 3). The a, b₁b₁ and b₂ items in Table 2 correspond to D – F + Hᵥ₁ – Hᵥ₂, Hᵥ, h² and Hᵥ₁ – Hᵥ₂ in Table 3, respectively. h indicates an estimate of Σhᵥ: the total sum of the dominances of the loci concerned. The significance of h was tested with h² and b₁ (Table 2). h was significantly positive in the lengths of the second and third leaves and culm. Actually, the most of the F₁'s showed higher values as compared with their midparents in these characters (Table 1). In the width of the first leaf, on the contrary, the most of the
F₁’s were lower than their midparents (Table 1), and h was significantly negative. In this character, the correlation coefficient between y₉ (the values of the parents) and W₉+V₉ was positively high, indicating consistently negative dominance of the loci concerned. Similar negative dominance was shown in the mean straw weight per culm (refer to the previous paper). Accordingly, it is pointed out that an F₁ tended to have culms longer, the second and third leaves longer, the first leaves narrower and lighter straw weight per culm than its midparent.

The number of genes controlling each character was estimated from two distinct formulae, i.e., hₒ/Hₒ and (the maximum parent value – the minimum parent value)²/4D (Table 3). The former gave lower estimates than the latter for the lengths of the first and second leaves and culm, since their correlation coefficients between y₉ and W₉+V₉ were low. The estimates by the latter varied from 1.14 of the first leaf width to 2.12 of the second leaf length. According to Mather and Jinks (1971), estimates by the latter tend to be lower than the true values. Hence, two or more genes may affect each character.

<table>
<thead>
<tr>
<th>Character</th>
<th>a</th>
<th>b</th>
<th>b₁</th>
<th>b₂</th>
<th>b₃</th>
<th>Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>1st leaf length</td>
<td>22.43**</td>
<td>8.24*</td>
<td>0.38</td>
<td>7.63*</td>
<td>10.29*</td>
<td>2.26</td>
</tr>
<tr>
<td>2nd leaf length</td>
<td>40.35**</td>
<td>5.10*</td>
<td>14.50*</td>
<td>3.62</td>
<td>4.41</td>
<td>1.64</td>
</tr>
<tr>
<td>3rd leaf length</td>
<td>54.99**</td>
<td>4.81**</td>
<td>14.21**</td>
<td>4.40*</td>
<td>3.26</td>
<td>1.15</td>
</tr>
<tr>
<td>Width of 1st leaf</td>
<td>5.441**</td>
<td>0.181*</td>
<td>0.641**</td>
<td>0.102</td>
<td>0.153*</td>
<td>0.048</td>
</tr>
<tr>
<td>Angle of 1st leaf</td>
<td>2099**</td>
<td>132</td>
<td>198</td>
<td>61</td>
<td>175</td>
<td>72</td>
</tr>
<tr>
<td>Culm length</td>
<td>416.7**</td>
<td>18.3**</td>
<td>37.6**</td>
<td>20.3**</td>
<td>12.8**</td>
<td>2.5</td>
</tr>
</tbody>
</table>

** Significant at the 0.05 and 0.01 levels, respectively.

Degrees of freedom of a, b, b₁, b₂, b₃ and error are 4, 10, 1, 4, 5 and 14, respectively.

<table>
<thead>
<tr>
<th>Character</th>
<th>D</th>
<th>H₁</th>
<th>H₂</th>
<th>h²</th>
<th>F</th>
<th>√Hₒ/D</th>
</tr>
</thead>
<tbody>
<tr>
<td>2nd leaf length</td>
<td>8.52**</td>
<td>5.42</td>
<td>4.89</td>
<td>4.52**</td>
<td>-2.80</td>
<td>0.80</td>
</tr>
<tr>
<td>3rd leaf length</td>
<td>15.4**</td>
<td>6.3*</td>
<td>5.1*</td>
<td>4.7**</td>
<td>1.2</td>
<td>0.64</td>
</tr>
<tr>
<td>Width of 1st leaf</td>
<td>1.59**</td>
<td>0.21**</td>
<td>0.19**</td>
<td>0.22**</td>
<td>0.10(*)</td>
<td>0.36</td>
</tr>
<tr>
<td>Angle of 1st leaf(5)</td>
<td>566*</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Culm length</td>
<td>92.5**</td>
<td>26.4**</td>
<td>23.6**</td>
<td>12.8**</td>
<td>-34.8**</td>
<td>0.53</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Character</th>
<th>Kₒ/Kₘ(1)</th>
<th>Hₒ/4H₁</th>
<th>h</th>
<th>r between y₉ &amp; (W₉+V₉)</th>
<th>hₒ²/H₂</th>
<th>(max. p. - min. p.)²/4D</th>
</tr>
</thead>
<tbody>
<tr>
<td>2nd leaf length</td>
<td>0.66</td>
<td>0.23</td>
<td>2.4</td>
<td>0.181</td>
<td>0.92</td>
<td>2.12</td>
</tr>
<tr>
<td>3rd leaf length</td>
<td>1.13</td>
<td>0.20</td>
<td>2.8</td>
<td>0.617</td>
<td>0.92</td>
<td>1.49</td>
</tr>
<tr>
<td>Width of 1st leaf</td>
<td>1.18</td>
<td>0.23</td>
<td>-0.5</td>
<td>0.881(*)</td>
<td>1.12</td>
<td>1.14</td>
</tr>
<tr>
<td>Angle of 1st leaf(5)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.30</td>
</tr>
<tr>
<td>Culm length</td>
<td>0.48</td>
<td>0.22</td>
<td>3.8</td>
<td>-0.148</td>
<td>0.54</td>
<td>1.64</td>
</tr>
</tbody>
</table>

1) (√4DHₒ+F)/(√4DHₒ-F), indicating the ratio of the number of dominant genes to the number of recessive genes in the parents.

2) Significant dominance was not shown.

(1) Significant at the 0.1, 0.05 and 0.01 levels, respectively.
Table 4. Correlation coefficients among leaf characters and culm length calculated by the parents (below the diagonal), and those calculated by the parents and their F₁'s (above the diagonal)

<table>
<thead>
<tr>
<th></th>
<th>Leaf length</th>
<th>1st leaf</th>
<th>Culm length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1st</td>
<td>2nd</td>
<td>3rd</td>
</tr>
<tr>
<td>1st leaf length</td>
<td>.68**</td>
<td>.73**</td>
<td>.68**</td>
</tr>
<tr>
<td>2nd leaf length</td>
<td>.90*</td>
<td>.85**</td>
<td>.64*</td>
</tr>
<tr>
<td>3rd leaf length</td>
<td>.82</td>
<td>.84</td>
<td>.78**</td>
</tr>
<tr>
<td>Width of 1st leaf</td>
<td>.62</td>
<td>.72</td>
<td>.95*</td>
</tr>
<tr>
<td>Angle of 1st leaf</td>
<td>.81</td>
<td>.80</td>
<td>.95*</td>
</tr>
<tr>
<td>Culm length</td>
<td>.97**</td>
<td>.95*</td>
<td>.74</td>
</tr>
</tbody>
</table>

** Significant at the 0.05 and 0.01 levels, respectively.

Table 4 shows correlation coefficients among the characters calculated by the parents (below the diagonal), and those calculated by the parents and the F₁'s (above the diagonal). All leaf characters highly correlated with culm length. Positive correlations were shown among all leaf characters. These indicated a trend that a short culm genotype had short, narrow and erect leaves, and vice versa. Similar correlation was shown in 32 varieties including the five parents (Murai et al., 1983). In order to explain this phenomenon, two different factors can be supposed: 1) genes which shorten culm have pleiotropic effects to shorten and erect leaves and vice versa, and 2) a short culm variety possesses distinct three gene groups which shortens culm, shortens leaves and erects leaves, respectively, while a long culm one possesses three gene groups of inverse effects. Murai et al. (1982) clarified by using isogenic lines that d-47 derived from IR-8 and other dwarf genes shorten and erect leaves as well as short culm. Although there is not any tangible evidence for whether 1) is true or 2), 1) is regarded as the principal factor at present.

**Literature Cited**

イネの葉部形質に関するダイアレル分析

村井 正之\textsuperscript{1}), 木下 俊郎\textsuperscript{2})・広瀬昌平\textsuperscript{1})

\textsuperscript{1}) 日本大学農業医学部，東京都世田谷区 〒 154
\textsuperscript{2}) 北海道大学農学部，札幌市 〒 060

北海道の5品種の片面交雑によるF\textsubscript{1}を用いて、葉身の形態的形質についてのダイアレル分析（Hayman 1954 \textit{ab}, Jones 1965）を行った。

すべての形質において、相加的遺伝子効果による分散（a）が優性分散（b）より顕著に大きかった（Table 2）。第2および第3葉身長において、h（各遺伝子座の優性の合計すなわち \sum h_i の推定値）は有意な正の値を示し（Table 3）、F\textsubscript{1}の多くはそれぞれの中間値の値より大であった（Table 1）。反対に、不育幅の優性は一致して負であり（Table 3）、F\textsubscript{1}の多くはそれぞれの中間値の値より小であった（Table 1）。

（最大値の値=最小値の値）\textsuperscript{2}/4D による各形質の関連遺伝子の推定数は、1.14～2.12であった（Table 3）。この式による推定数は過少になる傾向にある（Mather and Jinks 1971）ので、各形質には2対以上の遺伝子が関与していると考えられた。

全ての形質および稲長の相互関には高い正の相関関係がみられた（Table 4）。従って、短稲の F\textsubscript{1}もしくは親品種は短く細く直立的な葉身を有し、反対に、長稲のそれは長く幅広で下垂的な葉身を有する傾向にあった。