PATERNAL AND MATERNAL EFFECTS ON PROTEIN
AND OIL CONTENT IN SUMMER RAPE

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Comparisons among self- and cross-pollinated seeds from two summer rape (Brassica napus L.) cultivars, Midas and Tower, suggest that protein and oil contents of the seed are determined by the genotype of the plant which produces the seed. Pollen source also appears to have a slight effect on oil content. Comparisons among seed samples produced by the F1 and F2 progenies, derived from reciprocal crosses, indicate that protein and oil contents of the seed are controlled by nuclear genes and not by extranuclear determinants.

The paternal effect in plants is exhibited by differences among seeds borne on the same plant but developed from different sources of pollen. While East (1913) used the term “xenia” to describe the visible effect of alien pollen upon the F1 endosperm, Brink and Cooper (1947) applied the term “metaxenia” to these effects outside the embryo and endosperm. Non-visible effects of pollen on protein and oil contents of seed may be referred to as “xenia-like.” In the corn kernel, percent oil can be influenced by the source of pollen (Gilbert 1961; Garwood et al. 1970), but no such effect has been observed in flax (Yermanos 1960). The effect of pollen on the protein content of the developing seed has not been significant in corn (Gilbert 1961), common beans (Porter 1972), sunflowers (Pawlowski 1964), or soybeans (Singh and Hadley 1972).

A common type of genetic maternal effect in plants is cytoplasmic inheritance which persists through generations and can be unambiguously detected by differences between plants obtained from reciprocal crosses. Significant differences in percent oil have been reported between the reciprocal F1 plants of corn (Poneleit and Bauman 1970) and sunflower (Fick 1975). In corn, these differences did not persist in the F2 generation. In oats, Brown et al. (1974) found no significant difference in percent oil in seed from reciprocal crosses. Significant differences in the percent protein of seed have been observed between the reciprocal plants of soybean, in both the F1 and F2 generations (Singh and Hadley 1972). In common beans such differences did not persist in the F2 generation, indicating a maternal but not a cytoplasmic effect (Leleji et al. 1972). No cytoplasmic effect on percent protein has been found in wheat flour (Hsu 1968) or oats (Ohm 1972).

This paper deals with experiments designed to furnish information on paternal and maternal effects on percent oil and percent protein in rapeseed.
MATERIALS AND METHODS

Two summer rape (Brassica napus L.) cultivars, Midas and Tower, were used as low protein/high oil and high protein/low oil parents, respectively. Midas has been selected for higher percent oil and Tower for higher sum of protein and oil as a percentage of the seed, hereafter referred to as "sum."

Paternal Effect

Thirteen plants of each cultivar were selfed and reciprocally crossed in field. Percent protein in seed was determined for all plants and percent oil was obtained for 11 pairs of plants which produced sufficient seed for both analyses. Parental lines were compared by independent t-test, while paired t-test was used for other comparisons. Relative importance of the parents in conditioning the traits in the F1 seed was estimated by the standard partial regression coefficients (Snedecor and Cochran 1967), using the value of F1 seed as the dependent and those of the male and female parents as the two independent variables.

Maternal Effect

Seven sets of reciprocal crosses were made between the two parents and were advanced one generation under greenhouse conditions. The F1 and F2 seeds of each set were planted in the field in two replicates as described in a previous paper (Grami and Stefansson 1977). At maturity, 15 F1 plants and 25 F2 plants were taken at random from each plot, i.e. a total of 420 and 700 plants from each generation, respectively.

Protein content was determined by the Kjeldahl method and oil content by nuclear magnetic resonance (NMR). Both oil and protein analyses were done on the same subsample of oven-dried intact seed. The F1 and F2 generations were analyzed separately, with respect to the plot means, in a three-way (set, replicate and reciprocal cross) analysis of variance. The reciprocal plants within each replicate of each set were compared by an independent t-test.

RESULTS AND DISCUSSION

Paternal Effect

There were no significant differences in oil or protein content of F1 seed and self-pollinated seed borne on plants of the same cultivar (Table 1). However, there were significant differences in protein content between seed borne on Tower and Midas, regardless of whether they arose from self- or cross-pollination. The seed's own genotype might have had some effect on its oil content but the magnitude of the effect was small. Similar results have been obtained in soybeans (Singh and Hadley 1968).

The degree of dependence of the F1 seed upon either of the parents was estimated by standard partial regression coefficients. These coefficients (Table 1), representing the relative importance of each parent in expression of these traits in the F1 seed, were large between the F1 seed and maternal parent and were very small between the F1 seed and pollen parent.

The results suggested that percent protein in the F1 seed was determined by the genotype of the plant on which the seeds were produced. The preponderant influence

Table 1. Mean percent protein and percent oil, standard error, and standard partial regression coefficient for the selfed and reciprocally crossed seeds of two rapeseed cultivars

<table>
<thead>
<tr>
<th>Cross</th>
<th>Mean ± SE</th>
<th>SPRC</th>
<th>Percent protein</th>
<th>Mean ± SE</th>
<th>SPRC</th>
<th>Percent oil</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Midas</td>
<td>Tower</td>
<td>Midas</td>
<td>Tower</td>
</tr>
<tr>
<td>Midas × Midas</td>
<td>30.60 ± .36</td>
<td>.93</td>
<td>.93</td>
<td>.93</td>
<td>.93</td>
<td>.38</td>
</tr>
<tr>
<td>Midas × Tower</td>
<td>30.75 ± .40</td>
<td>.93</td>
<td>.04</td>
<td>39.58 ± .58</td>
<td>.93</td>
<td>.38</td>
</tr>
<tr>
<td>Tower × Midas</td>
<td>34.35 ± .40</td>
<td>.71</td>
<td>.71</td>
<td>37.83 ± .93</td>
<td>.01</td>
<td>.68</td>
</tr>
<tr>
<td>Tower × Tower</td>
<td>34.47 ± .50</td>
<td>.13</td>
<td>.47</td>
<td>36.69 ± .85</td>
<td>.01</td>
<td>.68</td>
</tr>
</tbody>
</table>

†Two means within a column which are not followed by the same letter are different at 0.05 level of significance. 
‡SE, standard error. 
§SPRC, standard partial regression coefficient.
of the female parent upon the oil percentage
of the seed was evident, although a small
effect of pollen source was also indicated.
The protein and oil-producing capacity of a
given genotype in rapeseed can be, there­
fore, sufficiently evaluated under open­
pollination conditions. Lack of pollen effect
on percent protein in rapeseed is in
agreement with the results obtained in other
crops. The expression of low percent
protein in the F1 corn seed has been
attributed to the size of the hybrid seed
which was larger than inbred seed (Leng et
al. 1951). Regarding percent oil, no im­
mediate effect of pollen has been observed
in any crop other than corn. Re-examining
some published corn data, Gilbert (1961)
concluded that xenia was of considerable
importance in percent oil; this has been
confirmed by Garwood et al. (1970).
However, our findings indicate that unlike
corn, controlled pollination is not required
in the genetic studies concerned with oil
content in rapeseed.

Maternal Effect
Analyses of variance for the parental, F1,
and F2 row means indicate that while the
parents were significantly different in per­
cent protein, percent oil, and their “sum,”
reciprocal crosses between these parents did
not differ for these traits in either the F1 or
F2 generation (Table 2).

Differences between reciprocal plants
were more closely examined by comparing
the means of reciprocals for each set in each
replicate separately, as suggested by Jinks
et al. (1972). Considering the fact that
Tower (P2) contained higher percent protein
than Midas (P1), if the main differences in
percent protein between reciprocals had all
positive signs (i.e. P2 × P1 > P1 × P2) one
would conclude that crosses resembled their
maternal parent. All negative signs for
reciprocal differences in percent oil (i.e. P2
× P1 < P1 × P2), however, would indicate
maternal effect, since percent oil in Midas
was higher than Tower.

Of the 14 differences between the means
of the F1 reciprocals for each character,
only one difference for protein, two for oil,
and two for their sum were significant
(Table 3). The fact that none of these
significant differences persisted in the F2
generation suggests that they could not be
due to unequal contributions of cytoplasmic
determinants from the parental gametes to
zygote. The likelihood that such transient
reciprocal differences may have arisen from
differences in maternal environment is very
low because they were not consistent in sign
and all but one belonged to the same set.

The direction of the cross did not affect
the percent oil, percent protein, or the sum
of these two components. Thus it is
concluded that nuclear genes, rather than
extranuclear determinants, condition the
expression of these traits. These results are
in agreement with those in oats (Brown et
al. 1974; Ohm 1972), but inconsistent with
those in soybeans (Singh and Hadley
1972) and sunflower (Fick 1975). The inconsis­
tency among some published reports could
be due to the transient effect of maternal
environment, which may decline in the next
generation, and/or to the inadequate
number of crosses sampled.

Table 2. Means and standard error of differences in percent protein, percent oil, and “sum” between two rape
cultivars and their reciprocal crosses in the F1, and the F2 generations

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Midas</th>
<th>Tower</th>
<th>P1×P2</th>
<th>P2×P1</th>
<th>(P1×P2)× (P2×P1)</th>
<th>SED†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Protein (%)</td>
<td>25.36</td>
<td>30.32***</td>
<td>.27</td>
<td>27.65</td>
<td>27.62</td>
<td>.20</td>
</tr>
<tr>
<td>Oil (%)</td>
<td>43.67***</td>
<td>41.68</td>
<td>.25</td>
<td>42.38</td>
<td>42.27</td>
<td>.13</td>
</tr>
<tr>
<td>“Sum”</td>
<td>69.03</td>
<td>72.00***</td>
<td>.18</td>
<td>70.03</td>
<td>69.89</td>
<td>.22</td>
</tr>
</tbody>
</table>

†SED, standard error of differences.
***indicates 0.001 level of significance.
Table 3. Mean differences and the associated standard errors for percent protein, percent oil, and their "sum" between reciprocal F1 plants obtained from two rape cultivars

<table>
<thead>
<tr>
<th>Sets</th>
<th>Replicate</th>
<th>Protein %</th>
<th>Oil %</th>
<th>&quot;Sum&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1</td>
<td>+.05 ± .48</td>
<td>-.27 ± .60</td>
<td>-.22 ± .29</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>+.01 ± .44</td>
<td>-.63 ± .90</td>
<td>-.62 ± .55</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>+.26 ± .33</td>
<td>-.45 ± .38</td>
<td>-.19 ± .23</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>+.34 ± .53</td>
<td>-.96 ± .78</td>
<td>-.62 ± .41</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>+.50 ± .39</td>
<td>+1.61** ± .51</td>
<td>+2.11** ± .37</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-1.58** ± .45</td>
<td>+1.45* ± .58</td>
<td>-.13 ± .40</td>
</tr>
<tr>
<td>4</td>
<td>1</td>
<td>-.60 ± .36</td>
<td>+.75 ± .48</td>
<td>+.15 ± .27</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-.16 ± .53</td>
<td>-.54 ± .77</td>
<td>-.70 ± .34</td>
</tr>
<tr>
<td>5</td>
<td>1</td>
<td>-.03 ± .34</td>
<td>-.50 ± .48</td>
<td>-.53 ± .31</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-.39 ± .44</td>
<td>-.10 ± .69</td>
<td>-.49 ± .42</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>+.80 ± .76</td>
<td>+.04 ± 1.22</td>
<td>+.84 ± .56</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>-1.02 ± .71</td>
<td>-.27 ± 1.08</td>
<td>-1.29* ± .51</td>
</tr>
<tr>
<td>7</td>
<td>1</td>
<td>+.47 ± .58</td>
<td>-.29 ± .85</td>
<td>+.18 ± .42</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>+.91 ± .54</td>
<td>-1.35 ± .83</td>
<td>-.44 ± .40</td>
</tr>
</tbody>
</table>

†Each value represents the mean difference between 15 plants in each cross, hence df = 28 for the non-paired t statistic. * and ** indicate the 0.05 and 0.01 levels of significance.

ACKNOWLEDGMENTS

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HSU, CHIN-SHENG. 1968. Inheritance of flour protein content and sedimentation value in diallel crosses among four wheat varieties. Diss. Abstr. 29: 2714B.


