Selection for time to maturity in soybean (Glycine max (L.) Merrill) and seed protein content of early maturing genotypes

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(With 3 figures)

Summary

F2-derived families from five different crosses between soybean genotypes of maturity groups 0 to 000 were evaluated for time to maturity in the F2-generation. Transgressions over the earlier parent’s maturity were observed in all populations. Broad sense heritability of time to maturity was moderately high with estimates ranging between 0.70 and 0.94. Selection for early maturity was effective both on individual plant and family basis, although late segregants could not be excluded completely by one generation of selection. A realised heritability of 0.66 was obtained after selection for earliness in single plants of the F2-generation, which indicates that selection for time to maturity can be practised during early generations of a pedigree breeding program. After selection for early maturity, variation in seed protein content was low between families within populations, whereas significant differences in protein content were found between the crosses investigated.

Key-words: Glycine max, soybean, time to maturity, heritability, seed protein content.

Selektion auf Reifezeit bei Sojabohne (Glycine max (L.) Merrill) und Proteingehalte von frühreifenden Genotypen

Zusammenfassung

Die F2-Nachkommenschaften aus fünf verschiedenen Kreuzungen zwischen Sojabohnen-Genotypen der Reifegruppen 0 bis 000 wurden in der F2-Generation hinsichtlich ihrer Reifezeit untersucht. Dabei wurden in allen Populationen Transgressionen über die Reifezeit des früher reifenden Elters beobachtet und Schätzwerte für die Heritabilität des Merkmals Reifezeit ermittelt, die im Bereich zwischen 0,70 und 0,94 lagen. Eine Selektion auf frühe Reife war sowohl an Einzelpflanzen als auch an Familien erfolgreich, die vollständige Eliminierung von zu spät reifenden Nachkommenschaften in einem einzigen Selektionsschritt war jedoch nicht möglich. Durch Selektion auf Frühreife an F2-

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Einzelpflanzen wurde eine realisierte Heritabilität von 0,66 erzielt, was die Möglichkeit einer Auslese auf frühe Reife während der ersten Spaltungsgenerationen bestätigt. Nach einer Selektion auf frühe Reifezeit erwies sich die Variation im Proteingehalt zwischen den Familien innerhalb der einzelnen Kreuzungen als relativ gering, womit die unterschiedlichen Kreuzungen insgesamt jedoch signifikant verschiedene Proteingehalte erkennen ließen.

Schlüsselworte: *Glycine max*, Sojabohne, Reifezeit, Heritabilität, Proteingehalt.

1. Introduction

Soybean (*Glycine max* (L.) Merril) is a short-day plant in terms of flowering and time to maturity, with reproductive responses to short-day photoperiods being quantitative rather than qualitative. Thus, cultivars of a given maturity group are adapted to a narrow range of latitude (FREDERICK and HESKETH 1994). Moreover, an interaction between day-length and temperature has been described in photoperiod-sensitive genotypes, and higher temperatures increase the rate of progress towards flowering (HADLEY et al. 1984). Additionally, in cool regions of Central Europe, temperature is considered to be even the most limiting factor of soybean cultivation (SOLDATI and KELLER 1985). Therefore, in breeding cultivars for a certain area of production, genotypes have to be selected which fit to the proposed region in their time to maturity. Consequently, early maturity is an important breeding goal and a prerequisite for adapting soybeans to short-season environments (ELOVSON 1984, SCHORI et al. 1988).

Flowering date and time to maturity are quantitative characters with a mainly additive mode of inheritance (BURTON 1987) and continuous segregation, with partial dominance of early or late maturity in progeny of particular crosses (GILKOL et al. 1980). In addition, five major loci with two alleles in each of them have been described to modulate flowering and maturity (PALLMER and KREN 1987, McBRAIN and BERNARD 1987). These loci affect the sensitivity to photoperiod (UPADHYAY et al. 1994) and have been used to develop well-performing determinate genotypes with timed flowering and maturity adapted to high latitude areas (SAINDON et al. 1990). In soybean improvement programs dealing with genotypes of early maturity groups, selection for time to maturity during segregating generations has been successfully practiced in single-seed descent (BYRON and ORF 1991) or pedigree selection procedures (JINLING and FANGLAN 1985, MOLARI et al. 1987) and moreover in mutation breeding programs (HODOSNE-KOTVICS and HESZKY 1994, ZACHARLIS 1978). Estimates of heritability for time to maturity were reported to be rather high in most of the populations analysed, indicating a significant role of heritable variation in this character (BURTON 1987, MAHMUD and KRAMER 1951, XU and WILCOX 1992).

Selection for time to maturity in early pedigree generations and estimates of heritability have rarely been reported from crosses involving maturity group 0 to 000 genotypes. Therefore, the objective of the present study was to evaluate the feasibility of selection for early maturity in segregating populations during a pedigree selection procedure. Subsequently, protein content of families selected for early maturity was assessed, because seed quality parameters are considered increasingly important in soybean.

2. Materials and methods

Preparation of genetic material

Segregating populations used in the present study were derived from the soybean crosses Dom×Apache, Dom×B152, Dom×Silvia, Dunajka×Apache and
Evans×Birka. Parent genotypes Dom (maturity group 0), Apache (0–00) and Evans (0), which are of North American origin, are registered cultivars in Austria (BUNDESAMT 1995); Silvia (00) is a cultivar released in Switzerland (SCHORI et al. 1988); B152 (I), Dunajka (0) and Birka (000) are experimental varieties. F₂-generations were grown in the field in 1992 and between 100 and 550 single plants were harvested separately from each combination without practising any selection. In order to examine the feasibility of selecting for early maturity in the F₂-generation, a subpopulation of Dom×Apache was established by visual selection for earliness on single plants at a selection intensity of 40 %. F₂-derived families of the different crosses were examined in 1993 (F₂:3) and after a selection step in 1994 (F₂:4).

Characters investigated

All characters reported were determined on a single row basis reflecting the average performance of approx. 15 to 30 individual plants. Time to maturity was expressed in days from sowing to full maturity (date when 90 % of the plants in a row were in The R8 stage according to FEHR and CAVINESS’S (1980) classification of soybean developmental stages). Similarly, flowering date was given as number of days from sowing to the beginning bloom stage (date when 10 % of the plants in a row had developed an open flower (R1 stage)). Plant height in cm was collected as one averaged reading per row after plants had reached their final length. Seed protein content is reported on dry matter basis and was determined from finely ground seed samples by near-infrared reflectance spectroscopy (NIRS) using an InfraAlyzer model 450 spectrophotometer and IDAS software (Bran & Luebbe, Norderstedt, Germany).

Experimental procedures and data analysis

Experiments were carried out in Gross Enzersdorf (Lower Austria, 15 km east of Vienna), which is characterised by chernozem-like medium heavy soils of a pH of 7.5 and continental climate with relatively dry summers and annual precipitation mean of 572 mm. F₂-derived families were sown in both the 1993 and 1994 seasons during the last week of April in single rows 2 m long and 60 cm apart.

In the 1993 trial, a total of 1119 F₂:3-families of the five different crosses was planted in unreplicated rows together with the respective parental genotypes, which were sown in randomly distributed rows in 7 to 10 replications each. In order to estimate broad sense heritabilities within crosses, unselected F₂:3-families were considered to represent the total phenotypic variation of a given population and variation within parent genotypes was utilised to assess environmental variation; the method by MAHMUD and KRAMER (1951) was adapted to the different F₂:3-families and heritability was calculated according to the formula

\[ h^2 = \frac{s^2_{F2:3} - s^2_{P1} \times s^2_{P2}}{s^2_{F2:3}} \]

in which \( h^2 \) denotes the heritability estimate and \( s^2 \) is the phenotypic variance of parents P₁, P₂ and F₂:3-families, respectively.

Furthermore, the effects of selection for earliness in the F₂-generation were studied in the subpopulation of the Dom×Apache cross, which was compared to the original population using an unpaired t-test; a “realised” heritability estimate was calculated from the difference in time to maturity between the
two populations, the standardized selection differential at 40% selection intensity and the phenotypic standard deviation.

After a visual selection for pod-set and early maturity (families maturing later than cv. Dom in 1993 were eliminated), a total number of 176 F2.4-families from all crosses was again planted in unreplicated rows in a completely randomised design in 1994. Cv. Apache which is an early maturity group 0 cultivar was used as a check variety to examine the response to selection for time to maturity. In order to investigate variation in protein content within as well as between crosses, protein content was determined from all families grown in the 1994 trial. Correlation coefficients between the 1993 and 1994 protein contents of selected families were calculated to estimate the magnitude of genetic variation for protein content within crosses; one-way analysis of variance (ANOVA) of the 1994 protein content data was conducted to examine the significance of variation between the different crosses using F2.4-families within each cross as replications.

3. Results

Time to maturity

The distributions of time to maturity of F2.3-families including the respective parental means are shown in figure 1 for the five different populations. Transgressions of up to 16 days over the earlier or later parent's time to maturity could be found in the populations investigated, particularly in the Dom×B152 and

![Distribution of time to maturity (days from sowing to R8 stage) in F2.3-families of different crosses and maturity date of the respective parental genotypes (indicated by arrows).](image-url)
Dunajka×Apache crosses with respect to earliness. Comparing population means and mid-parent values, partial dominance of late maturity could be observed in some combinations such as Dom×Silvia, whereas maturity of the Dom×B152 population was 3.5 days earlier than it's mid-parent value (data not presented). Broad sense heritabilities of flowering date, plant height and time to maturity are given in table 1 for the different crosses. Heritability of flowering date and time to maturity were at a similar level ranging from 0.70 up to 0.94, whereas the estimates for plant height were slightly lower. Highest estimates of heritability were found within the Dom×Silvia population for all characters investigated. This indicates the considerable genetic diversity between these two parents, which is also evident from figure 1 for time to maturity.

Table 1

<table>
<thead>
<tr>
<th>Cross</th>
<th>Flowering date</th>
<th>Plant height</th>
<th>Time to maturity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dom×Apache</td>
<td>0.76</td>
<td>0.56</td>
<td>0.70</td>
</tr>
<tr>
<td>Dom×B152</td>
<td>0.76</td>
<td>0.87</td>
<td>0.79</td>
</tr>
<tr>
<td>Dom×Silvia</td>
<td>0.91</td>
<td>0.88</td>
<td>0.94</td>
</tr>
<tr>
<td>Dunajka×Apache</td>
<td>0.76</td>
<td>0.47</td>
<td>0.86</td>
</tr>
<tr>
<td>Evans×Birka</td>
<td>0.75</td>
<td>0.80</td>
<td>0.82</td>
</tr>
</tbody>
</table>

Selection for earliness

A moderate selection for early maturity on single plants in the F$_2$-generation was effective for the population Dom×Apache, as demonstrated in figure 2. The frequency of late families was clearly reduced, although a few families with a time to maturity of more than 140 days were still present in the selected population. In table 2, mean values of the original population and the selected population are given for different characters: Selection for time to maturity significantly improved earliness of the population by 3.41 days; flowering occurred 1.33 days earlier and the period from R 1 to R 8 (reproductive period) was shortened by 2.08 days as a result of indirect selection. Plant height was not affected significantly by selection for early maturity; and lodging was not observed in any of the families. Subsequently, a realised heritability was calculated from the difference in time to maturity between the two populations resulting in an $h^2$ of 0.66.

Fig. 2: Distribution of time to maturity (days from sowing to R8 stage) in F$_2$-families of an unselected population and a population selected for early maturity in F$_2$ from the cross Dom×Apache.
Table 2
Effects of selection for early maturity in the F2-population on different characters of F2:3-families in the cross Dom×Apache

<table>
<thead>
<tr>
<th>Character</th>
<th>Population means</th>
<th>Difference/ significance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>unselected control population (n=538)</td>
<td>selected population (n=109)</td>
</tr>
<tr>
<td>Flowering date (days)</td>
<td>52.37</td>
<td>51.04</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>69.24</td>
<td>68.53</td>
</tr>
<tr>
<td>Time to maturity (days)</td>
<td>137.28</td>
<td>133.87</td>
</tr>
<tr>
<td>R1 to R8 (days)</td>
<td>84.91</td>
<td>82.83</td>
</tr>
</tbody>
</table>

(n.s. = not significant; **, ***: significant at the 1 and 0.1 % level according to t-test)

Selection for time to maturity in F2:3-families planted in single row plots in 1993 improved earliness of most of the selected populations in the 1994 season, as demonstrated in table 3; in order to verify the responses to selection, cv. Apache (maturity group 0-00) was used as an internal control genotype and time to maturity was expressed as a percentage of families earlier than Apache, because the original populations were not planted any longer in 1994. The selected population of the cross Dunajka×Apache was maturing later than the original population, which was due to a considerable number of families later than Apache which had been selected because of favourable pod-set.

Table 3
Percentages of F2-derived families with earlier time to maturity than Apache in 1993 and in 1994 (after selection for earliness)

<table>
<thead>
<tr>
<th>Cross</th>
<th>1993 (F2:3-generation) number of families earlier than cv. Apache</th>
<th>1994 (F2:4-generation) number of families earlier than cv. Apache</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dom×Apache</td>
<td>538</td>
<td>69</td>
</tr>
<tr>
<td>Dom×B152</td>
<td>110</td>
<td>11</td>
</tr>
<tr>
<td>Dom×Silvia</td>
<td>168</td>
<td>18</td>
</tr>
<tr>
<td>Dunajka×Apache</td>
<td>107</td>
<td>34</td>
</tr>
<tr>
<td>Evans×Birka</td>
<td>87</td>
<td>24</td>
</tr>
</tbody>
</table>

Seed protein content of early maturing genotypes

Seed protein content of selected families was in the range of 38.5 to 44.5 % in 1993, whereas in 1994 clearly higher protein contents between 40.4 and 47.5 % were found in the same genetic materials. Phenotypic coefficients of correlation between protein contents of the selected families in 1993 and 1994 were low (r=0.05 to 0.26) and not significant within each of the five crosses investigated. This indicates that after selection for early maturity, a recoverable genetic variation in protein content was not present across the two years within the population. However, significant differences (F-test, P<0.05) in protein content were identified between the different populations in 1994 by an analysis of variance after verifying of an approximate normal distribution of the percentage data using the KOLMOGOROV-SMIRNOV test. Population means of all crosses with cv. Apache as a parent genotype and of cross Dom×Silvia were significantly higher in protein content than the means of the remaining two populations (LSD-test at P=0.05). An overview of the variation in protein content as
observed in 1994 is given in figure 3 by a multiple box-and-whisker plot of the different populations. After selection for early maturity, significant correlations have not been found between time to maturity and protein content in any of the populations investigated.

4. Discussion

Early maturity is an important characteristic of soybean genotypes for cultivation in short season and high latitude environments (Soldati and Keller 1985). Time to maturity is a quantitative trait with mainly additive inheritance (Burton 1987), although a few major genes (Palmer and Kilen 1987, McBlain and Bernard 1987) as well as partial dominance of early or late maturity in heterozygous populations (Gilioli et al. 1980, Bernard 1971) have been reported for this character. A mainly additive inheritance of time to maturity is also suggested from the progeny distributions and the transgressive segregations observed in most crosses of the present study (figure 1). Similar transgressions to both earlier and later maturity than parents have been reported from crosses between early maturing genotypes by Jinling and Fanglan (1985), whereas in the genetic materials analysed by Saindon et al. (1990) transgressive segregation was influenced by the allelic configuration at the \( E_1 \) and \( E_4 \) loci of maturity. The presence of major genes affecting time to maturity in crosses such as Dom \( \times \) Silvia or Dunaika \( \times \) Apache cannot be excluded, because irregularities in the distributions are obvious for this character (figure 1). However, the genetic constitution of the parental genotypes is unknown with respect to maturity genes; furthermore, irregular distributions in time to maturity could partly also be due to a period of cold weather during the first week of September in 1993, which reduced the percentage of families maturing between days 125 and 127 for all crosses (figure 1).

Heritability of time to maturity as well as of other developmental characters in soybean were reported to be high in most studies (Burton 1987). The high estimates of heritability for time to maturity found in the present investigation have to be considered as broad sense estimates, because the material analysed
had been derived from F2-populations. Although actually in F3, dominance
effects still present within some of the families could have added bias towards
an overestimation of heritability, as pointed out by CAHANER and HILLEL (1980).
Furthermore, the heritability estimates presented were taken from an experi­
ment conducted in one environment only, which has to be considered as an
additional source of overestimating heritability, because variance due to geno­
type×environment interaction cannot be separated from purely genetic vari­
ance. However, the realised heritability of 0.66 obtained from the selection
experiment in Dom×Apache is not strikingly smaller than the estimate
reported in table 1, which suggests that both the effects of non-additive genetic
variance as well as variance due to genotype×environment interaction were
small.

Selection for time to maturity was effective both in F2-plants and F2:3-
families, which is of considerable importance if early maturity has to be
selected in segregating generations during a pedigree breeding procedure.
Similar results in selection for earliness on a plant or family mean basis of a
Hodgson×Dunajka cross were also reported by MOLARI et al. (1987). As dem­
onstrated in figure 2, selection can be applied at the low intensity of 40 % in
an early generation by reducing extremely late segregants. Thus, genetic vari­
ation in seed yield and other agronomic characters can be retained for an
evaluation in subsequent generations. However, late segregants were not
eliminated completely after one step of selection (figure 2), which could be
due to incorrect determination of maturity on the individual plant basis, as
pointed out by BYRON and ORF (1991) with respect to selection in single-seed
descents.

Seed protein content of selected families was rather high in all crosses due to
environmental effects. In the genetic materials investigated, variation in pro­
tein content was small within crosses after the selection for early maturity.
However, significant variation in protein content was present between the dif­
ferent crosses: all populations with cv. Apache as a parent genotype were in the
high protein group, which is in good agreement with results of public trials
across a large number of environments in Austria attributing Apache a clearly
higher protein content than other genotypes of similar maturity groups (LUF­
TENSTEINER and PUTZ 1994). These findings indicate that only a moderate
enhancement of protein content can be expected from conventional breeding
programs with early maturing materials. If an improvement of protein content
is desired for genotypes of these maturity groups, specific selection programs
involving high protein donors (McKENDRY et al. 1985) or recurrent selection
(XU and WILCOX 1992) would be required.

The results of the present investigation clearly suggest that selection for time
to maturity in soybean can be accomplished during the first generations of a
pedigree breeding procedure. However, subsequent selection for seed quality
characters such as protein content would not be effective within the crosses
analysed which advocates specific programs in order to match such breeding
goals.

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References


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