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Inheritance of legumin and albumin contents in a cross between round and wrinkled peas

H. E. Schroeder and A. H. D. Brown
CSIRO, Division of Plant Industry, G.P.O. Box 1600, Canberra, A.C.T. 2601, Australia

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Summary. Legumin and albumin are the fractions of pea seed proteins preferred to vicilin because of their high sulfur amino acid contents. The joint inheritance of legumin and albumin contents was studied in a cross between to contrasting lines of peas – one with high legumin and low albumin, and the other with low legumin and medium to high albumin. Single seed determinations were made in the parental, F_1, F_2 and backcross generations using rocket immunoelectrophoresis. In the non-segregating generations (P_1, P_2 and F_1), legumin and albumin contents were negatively correlated ($r = -\cong 0.50$). The estimates of correlation coefficients in the segregating generations (F_2, BC_1 and BC_2) were also about – 0.5. However, the two estimates based on the round and on the wrinkled seeds separately in the F_2 generation were not significantly different from zero. At least four individual round F_2 seeds showed the desired recombination of high legumin with high albumin indicating that the unfavorable correlation can be broken. In this cross legumin content showed predominantly additive genetic variation whereas the dominance variance was the largest component for albumin content. A combined "relative sulfur index", proposed as a convenient measure for selection, showed a narrow sense heritability of 47%. In general these results support the view that sulfur amino acid content of peas can be improved by breeding, but that the required selection regime must take both legumin and albumin content into account.

Key words: Speed proteins- Legumin – Albumin – Heritability – Pisum – Pea

Introduction

The seed proteins in pea (*Pisum sativum* L.) seeds are made up of the storage globulins legumin and vicilin together with the albumins. Globulins account for 65–80% and albumins for 20–35% of the extractable protein of pea cotyledons (Schroeder 1982). The legumin, vicilin and albumin contents are genotype-specific but also environment-dependent (Füredi 1970; Bajaj et al. 1971; Gottschalk et al. 1975; Davies 1976, 1980; Przybylska et al. 1977; Thomson et al. 1979; Randall et al. 1979). Of the storage proteins, legumin has a higher sulfur amino acid content than vicilin and is therefore a more desirable protein fraction in terms of animal nutrition. It appears then, that sulfur amino acid content could be increased by genetically altering the proportions of storage proteins, i.e., raising legumin content at the expense of vicilin content. However, the albumins, as a protein fraction, have a considerably higher sulfur amino acid content than legumin with an overall more favourable amino acid profile than the globulins (Bajaj et al. 1971; Hurich et al. 1977; Boulter and Derbyshire 1971) and they are a quantitatively significant protein fraction. Furthermore it was previously found (Schroeder 1982) that legumin and albumin contents of a diverse set of lines are negatively correlated ($r = -0.76$) indicating that protein quality, if assessed in terms of sulfur amino acid content, cannot be improved by raising only the legumin content. The aim then should be to break the negative correlation and to combine high levels of legumin with high levels of albumins. Therefore, a realistic assessment of the prospects of increasing protein quality in peas depends on an understanding of the joint genetic control of legumin and albumin contents.

The purpose of this experiment was to study the joint inheritance and heritability of legumin and albumin contents in *P. sativum*. The results of the genetic analysis show that to be successful, breeding for increased protein quality must take account of both these sources of sulfur amino acids.

Materials and methods

Plant material

Crosses were made between a low legumin, medium to high albumin, wrinkled seeded line (Parent 1), and a high legumin, low albumin, round seeded line (Parent 2). Parent 1 was cv. 'Greenfeast', the Canberra control line PI/G 086 (Plant Industry/Genetics). Parent 2 was PI/G 307 (*Pisum* Genebank, Weibullsholm no. WL 110, Kungsärt). Seeds from parent lines were harvested only from those plants used in reciprocal crosses for the production of F_1, BC_1 and BC_2 generation seed. Cross combinations were made in both directions. F_2 generation seed was represented by seeds borne on F_1 plants. The characters measured were seed weight, percent extractable protein and legumin and albumin contents as percentages of extractable protein.

All plants were grown in a sand, loam, peat moss mixture (1 : 1 : 1) in 23 cm pots, with complete fertilizer added, in a greenhouse under natural light. The temperature range was 18 °C (night) to a maximum of 24 °C (day). Seed was harvested from completely desiccated plants, air-dried to a moisture content of 6.5–7.5% and then weighed.

Buffer extractable protein

Single seeds were dehulled and the cotyledons milled to a fine flour passing through a 0.2 mm screen. Duplicate samples of 50 mg flour per seed were extracted twice with 0.5 ml TBE extraction buffer (0.5 M tris (hydroxymethyl) aminomethane, 0.01 M ethylene diaminotetraacetic acid, titrated with boric acid to pH 9.2 containing 1 mM phenylmethyl-sulfonylfluoride). After vortexing, the samples were put on an end-over-end shaker for 30 min ast room temperature. The homogenate from each flour sample was centrifuged at 20,000 g for 20 min at 5 °C. Aliquots of the supernatant were used directly for protein determinations by biuret (Goa 1953) and to measure legumin and albumin contents.

Determination of legumin and albumin contents

Legumin and albumin contents as percentages of total extractable cotyledonary protein from flour were determined by Laurell's rocket immunoassay (Weeke 1973) using specific antisera raised in sheep, against purified legumin and albumin protein fractions. Samples (10 µl of single seed extracts were applied to wells cut into agarose gels (0.9%) into which either antilegumin or antialbumin serum had been mixed before cooling. Standards of pure legumin (9–19 µg) and pure albumin (7–19 µg) were included in the respective gels. The distance from the origin to the tip of the precipitin line was proportional to the amount of legumin in the samples. Rocket immunoelectrophoresis of the albumin fraction resulted in a rocket with 5–7 precipitin lines. However, the height of the major line of the rocket was directly proportional to the albumin concentration of albumin standards and albumin in the samples tested. By reference to a standard curve plotted for each gel, the amount of either legumin or albumin in single seed extracts was determined and expressed as percent of extractable protein. The duplicate extracts from each seed provided replicates of each variable legumin and albumin. Subsequent computations used the means of these two replicates.

Relative sulfur index

By using sulfur amino acid data from the literature (Casey and Short 1981; Hurich et al. 1977; Boulter and Derbyshire 1971) and percentages of legumin, vicilin and albumin, it can be calculated that most lines of peas differ little if at all in sulfur amino acid content (Schroeder 1982). This finding led us to calculate a relative sulfur index value for each of the seeds analysed in this cross. The sulfur index is proportional to the sum of $1.40 \times$ legumin %, $0.38 \times$ vicilin %, and $3.53 \times$ albumin %. Since the three fractions account for all the extractable cotyledonary protein this relationship can conveniently be expressed as – relative sulfur index = legumin % $+ 3.1 \times$ albumin %.

Genetic analysis

Genetic analysis was performed on the following characters; seed weight, protein content, the concentrations of the protein fractions legumin and albumin and the calculated relative sulfur index value. The additive (D) and dominance (H) genetic components of variance, and the environmental (E) component, as well as the narrow and broad sense heritabilities for each character were calculated by standard procedure (Mather and Jinks 1971). These used the generation variances for the parental lines, the two reciprocal F_1's the four backcrosses and the two F_2's. The four backcrosses arose because each of the two reciprocal F_1's were used as either male or female parents in backcrosses. In generations segregating for round versus wrinkled seed (backcrosses and F_2's) each seed was classified for seed type and the means and variances for all characters computed first within seed types. In backcrosses every seed harvested was analysed. In the F_2's all seeds harvested (total of 759) were grouped into round and wrinkled phenotypes to determine the phenotypic ratio. However, equal numbers of round and wrinkled seeds, taken at random from the two groups, were analysed. The means for each of the segregating generations were derived by averaging these groups weighted by the expected ratio. The variances of these whole populations included both the variation within seed phenotypes and the variation among seed phenotypes.

Results

Legumin and albumin contents

Determination of legumin and albumin content by rocket immunoelectrophoresis of a number of single seed extracts of P_1, P_2, F_2's and pure legumin and albumin standards are shown in Fig. 1 a, b.

In rockets of legumin standards, a second (minor) rocket is observed which is not seen in seed extracts. Presumably the concentration of this legumin component is too low in seed extracts to give a reaction. Heterogeneity in the albumin fraction is indicated by the number of minor rockets within the major rocket. The antiserum against albumins was made against an equal mixture of pure albumins from 20 lines of peas; this explains differences observed in the intensity of the minor rockets of standards and of seed extracts of parents and crosses. But chemical analyses of albumin contents and globulin to albumin ratio determinations (Schroeder 1982) of all the lines tested so far (data not shown) indicated that the height of the major rocket is proportional to the albumin concentration in protein extracts. A calibration curve showing the relationship between amounts of legumin and albumin standards

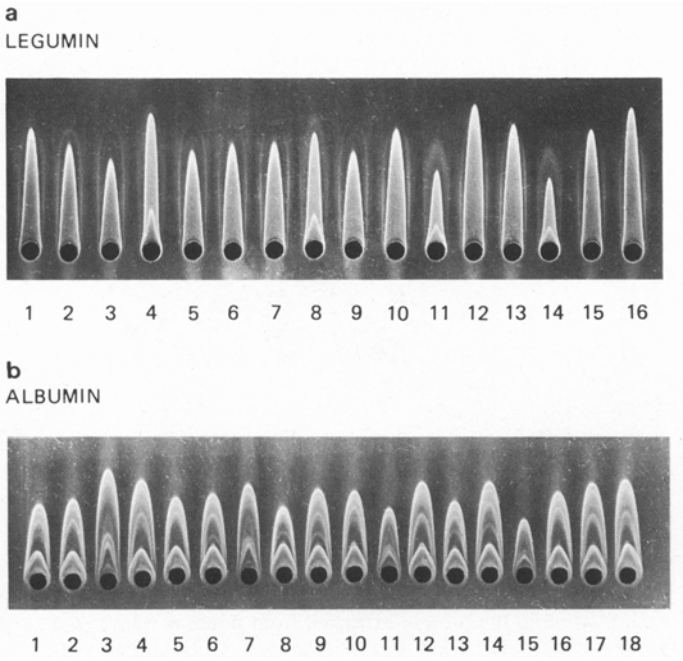

Fig. 1 a, b. Determinations of legumin and albumin contents by rocket immunoelectrophoresis. **(a)** rockets; *4, 8, 11* and *14* are legumin standards, *3* and *5* are Parent$_1$, *13* and *15* are Parent$_2$, others the F$_2$'s. **(b)** rockets; *3, 7, 11* and *15* are albumin standards, *4* is Parent$_1$, *8* is Parent$_2$, others are F$_2$'s

and the length of the immunoprecipitates (rockets) formed are shown in Fig. 2.

Segregation of round versus wrinkled

The present cross segregated for the classic character round versus wrinkled seeds in the expected 3 : 1 ratio in the F$_2$'s (572 : 187, $x^2 = 0.0295$). From the standpoint of seed protein fractions this major gene difference complicated the analysis. The choice of parents was largely determined by results from a previous survey of over 100 *P. sativum* lines which found that high legumin content was associated with round seeds while high albumin content was associated with wrinkled seeds. Furthermore, the wrinkled phenotype can be due to recessivity at either the r_a locus on chromosome 7 or at the r_b locus on chromosome 3. The r_a locus is linked to the structural gene for legumin on chromosome 7 (Davies 1980; Matta and Gatehouse 1982), so it was necessary to establish whether the wrinkled locus of 086 was also on chromosome 7. A test cross between wrinkled (r_br_b chromosome 3, PI/G 305) and wrinkled (*rr* 086) showed the wrinkled allele of 086 to be of the r_ar_a type on chromosome 7.

Generation means and standard deviations

The generation means with standard deviations of the four measured characters and sulfur index are given in Table 1. Seed weight is dominated by the *R/r* gene. Legumin and albumin percentage means in reciprocal F$_1$'s were close to the midparent value although the direction of the cross had some bearing; legumin was higher and albumin lower when P$_2$ was the female parent. In the segregating populations the genes for round versus wrinkled markedly affected the levels of legumin and albumin. As shown in Table 1 and seen in more detail in Fig. 3 higher legumin was associated with the round phenotype (*R-*) while higher albumin is associated with wrinkled (*rr*) in F$_2$ populations. This result differs from BC$_1$ populations (Table 1, Fig. 4), where in both *Rr* and *rr* populations two doses of 086 (P$_1$) caused lower legumin but higher albumin levels.

The effect of the major gene round versus wrinkled

The variation in legumin and albumin content of protein extracts from 141 individual F$_2$ seeds are shown in Fig. 3. For comparison, the mean values of these two characters for P$_1$, P$_2$ and reciprocal F$_1$'s are also shown.

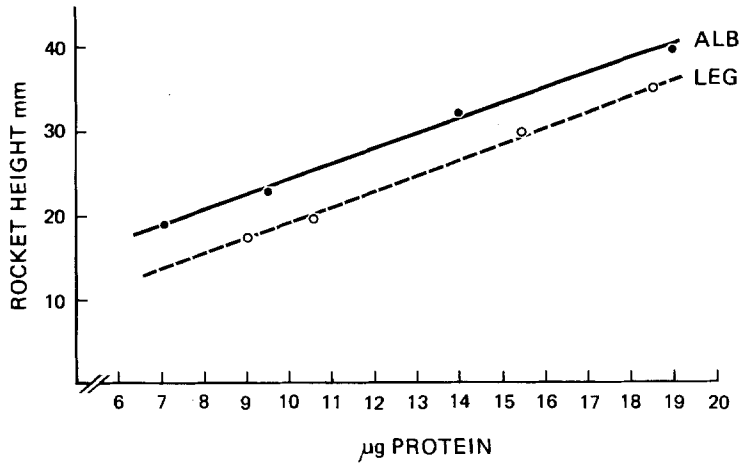

Fig. 2. Standard curves of legumin and albumin. Rocket height is proportional to the concentration of legumin and albumin in the total protein extracted from flour

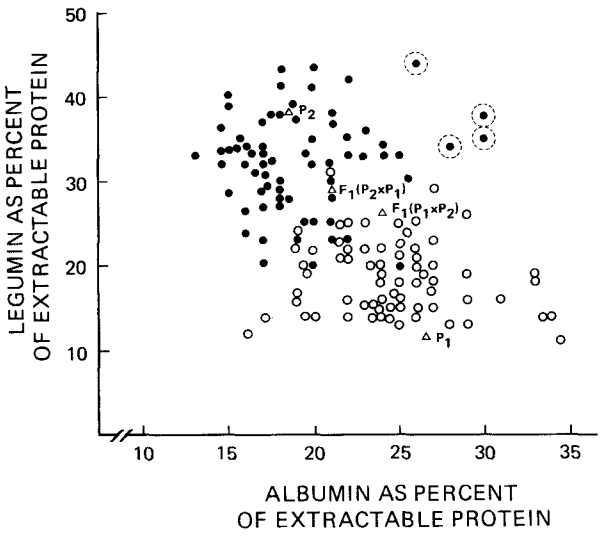

Fig. 3. Relationship of legumin and albumin contents of individual F_2 seeds. Results are expressed as the percentages of each fraction in the protein extracted from flour; ● round (*R*-) phenotypes, ○ wrinkled (*rr*) phenotypes. Correlation coefficients: $r = -0.513$ $P<0.001$, *R*-phenotypes only $r = -0.040$, *rr* phenotypes only $r = -0.154$

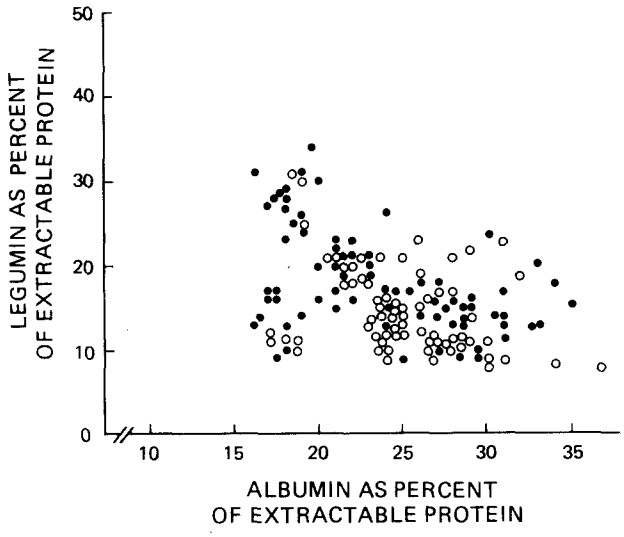

Fig. 4. Relationship of legumin and albumin contents of individual BC_1 seeds. Results are expressed as the percentages of each fraction in the protein extracted from flour; ● round (*R*-) phenotypes, ○ wrinkled (*rr*) phenotypes. Correlation coefficient $r = -0.419$ $P<0.01$

Table 1. Means and standard deviations (SD) of seed and protein characters in various generations of the cross between *Pisum satiuvm* cv. 'Greenfeast PI/G086' and PI/G307

	Seed phenotype	Seed wt		Seed protein %		Legumin %		Albumin %		Sulphur index		Sample size
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
P_1 = 086	*rr*	295	19	20.6	1.5	11.3	1.3	26.3	2.2	93	6	28
P_2 = 307	*RR*	381	21	20.2	1.5	38.2	3.6	18.7	1.9	96	5	28
086 × 307	*Rr*	389	16	20.9	1.1	25.8	1.8	24.0	2.2	100	6	14
307 × 086	*Rr*	357	10	19.9	0.7	29.0	2.4	21.4	1.2	95	4	14
F_2												
086 × 307	*rr*	342	23	20.6	1.0	17.4	4.3	26.2	4.1	99	12	34
307 × 086	*rr*	349	28	22.2	1.2	19.6	4.3	23.1	3.0	91	11	36
086 × 307	*R–*	382	19	19.7	0.7	32.2	6.1	18.1	3.4	88	12	35
307 × 086	*R–*	398	26	20.7	1.0	32.7	5.1	20.5	3.6	96	13	36
BC_1												
086 × (086 × 307)	*rr*	292	16	20.2	0.9	13.6	6.0	27.4	4.5	99	14	20
086 × (307 × 086)	*rr*	349	23	21.4	1.3	12.6	5.4	27.5	4.9	98	13	13
(086 × 307) × 086	*rr*	400	39	20.5	0.6	20.4	6.4	25.7	4.7	100	10	8
(307 × 086) × 086	*rr*	370	25	20.4	0.9	14.4	3.4	23.7	3.0	89	9	21
086 × (086 × 307)	*Rr*	294	19	19.3	0.6	16.4	5.7	26.0	4.3	97	12	25
086 × (307 × 086)	*Rr*	373	28	19.3	1.2	15.9	3.2	27.2	4.2	100	11	17
(086 × 307) × 086	*Rr*	415	39	19.2	0.7	19.0	8.1	23.9	7.5	93	24	7
(307 × 086) × 086	*Rr*	396	27	19.8	0.8	22.3	6.9	18.6	1.6	80	9	24
BC_2												
307 × (086 × 307)	*R–*	363	35	19.7	1.0	27.1	5.2	18.3	3.1	84	8	20
307 × (307 × 086)	*R–*	359	26	19.7	0.7	28.2	3.6	16.3	1.5	79	6	26
(086 × 307) × 307	*R–*	378	25	19.6	1.1	21.2	6.7	19.6	4.0	82	7	36
(307 × 086) × 307	*R–*	378	21	19.8	0.6	23.5	4.6	19.6	2.1	84	8	32

Round and wrinkled F_2's separate into two almost distinct groups. The previously established negative correlation between legumin and albumin content among diverse genotypes (Schroeder 1982) was again apparent in this segregating population, $r=-0.513$, $P<0.001$. On the other hand the joint distribution of legumin and albumin within the genetically uniform populations (P_1, P_2, F_1) resulted in correlation coefficients of $r=-0.53$, $r=-0.50$ and $r=-0.56$, respectively; all these estimates were statistically significant at the $P<0.01$ level. Thus, environmental variation can cause a negative correlation between legumin and albumin. However, this is not the sole cause of the correlation in the F_2 generation because the phenotypic variances of legumin and albumin are much greater in the F_2 generation than in P_1, P_2 and F_1 generations (Table 2).

When the correlation coefficients were calculated separately for the two F_2 subpopulations, the round phenotpyes had $r=-0.040$ and the wrinkled $r=-0.154$, i.e, they were close to zero and within these subpopulations legumin and albumin behaved like independent characters. This contrasted with the behavior of legumin and albumin in the BC_1 populations (Fig. 4), which showed no difference in segregation patterns between round and wrinkled subpopulations. Two doses of P_1 (086) caused lower legumin but high albumin population means (Table 1) in this generation. In BC_2 populations with all round seeds, two doses of P_2 (307) caused low albumin and lower than expected legumin levels. A significant negative correlation ($r=-0.657$ $P<0.001$) was observed.

Genetic variances and heritability

In this cross legumin content is controlled largely by genes with additive effects whereas albumin content is much more influenced by dominant genes (Table 2). For both legumin and albumin contents, the additive component is zero when the estimates are based on only the subpopulation of round seeds from the segregating generations. This arises because the variances of legumin and albumin contents in the F_2 generation are markedly less within the round subpopulation than for the whole generation whereas the BC_1 variances are not so affected. Compared with the F_2 generation, two doses of P_1 (086) reduced the variance of legumin content but increased the variance of albumin content, possibly indicating a pleiotropic effect of wrinkled (*rr*). The character sulfur index was different to both legumin and albumin content. Its inheritance in this cross showed both additive and dominance effects. Further, when the data from the round seeds are considered alone, the estimates of additive variance and heritability are not different from those based on all seeds. If legumin and albumin were independent characters, the variance for sulfur index in any generation should be predictable as the sum of variance of legumin content plus $(3.1)^2$ times the variance of albumin content. The theoretical estimates are 248 for the whole F_2 population and 162 for the round F_2 subpopulation. The difference (248–170) arises from the negative correlation between legumin and albumin (Fig. 3). For the round subpopulations however, there was no difference be-

Table 2. Generation variances, variance components and heritability estimates for seed protein characters

Generation	Legumin content		Albumin content		Sulphur index	
P_1	1.6		5.1		42	
P_2	13.3		3.7		27	
F_1	7.0		4.8		29	
F_2[a]	64.7	32.0	19.1	13.5	170	178
BC_1[a]	40.6	41.7	25.5	28.7	192	222
BC_2	35.4		10.3		55	
Variance components						
D-Additive	106.8	0	4.8	0	186	159
H-Dominance	16.4	113.4	48.4	60.8	180	284
E-Environmental	7.2	10.2	4.6	4.3	32	28
Heritability						
h^2 narrow	82	0	8	0	47	34
h^2 broad	94	92	92	93	93	94

where $E=(P_1+P_2+2F_1)/4$
$D=4F_2-2(BC_1+BC_2)$
$H=2(BC_1+BC_2)-D-4E$

[a] In the two generations segregating for round (*R*–) versus wrinkled (*rr*), two variance estimates are given. The first is a combined estimate over both phenotypes, the second is for variances within the round phenotype. This leads two sets of genetic statistics

tween the theoretical variances. These results clearly support selection based on sulfur index.

Discussion

In *Pisum*, the two seed protein fractions rich in sulfur amino acids legumin and albumin, were previously found to be negatively correlated (Schroeder 1982). Hence seed protein quality may not be improved simply by altering the proportions of the major storage proteins, i.e., by increasing legumin at the expense of vicilin. This raises the important question, can the correlation be broken genetically and recombinant genotypes be identified and selected that combine high legumin with high albumin contents.

The inheritance of legumin and albumin content in peas was studied in a cross in which the parents had similar protein content, but differed in seed weight, seed type, and legumin and albumin content (Tables 1 and 2). Seed weight and protein content were of lesser interest in this study. Seed weight is important in determining yield and protein yield, but this cross was not set up to study this variable. Inheritance of protein content has already been studied in more appropriate crosses (for example see: Slinkard 1980; Weber 1981; Swiecicki 1981). Little variation for this variable existed in this cross.

In this cross it was found that the genes for seed type (*R*/*r*) had a major effect on seed protein composition, namely legumin and albumin contents (Figs. 3 and 4). Variation at this locus also had a marked effect on estimates of the components of variances for legumin content, albumin content and sulfur index (Table 2). Out of a total of 141 F_2 generation seeds four seeds with the round phenotype (circled, Fig. 3) were identified which apparently combine relatively high levels of legumin and albumin. No comparable phenotypes were found in the wrinkled F_2 subpopulation indicating the confounding effect of the *rr* genotype on seed protein composition.

The combined high legumin and high albumin contents of the four F_2 progeny indicate that total sulfur amino acid content should be considerably increased in the protein of these seeds. Total sulfur estimates have been proposed as coarse indicators of S-amino acid levels (Boulter et al. 1976). In this case, measurements of total sulfur, 0.233% for the four F_2's, 0.206% for P_1 and 0.220% for P_2, indicate an increase in S-amio acid content in the four F_2 seeds. The mean value of the relative sulfur indices for the four F_2's was 126.6. This represents a substantial increase over the values of 93 for P_1, 96 for P_2, 93.5 for the F_2 populations and 93.5 ± 7.8 for the 45 lines of peas previously examined. The sulfur index is a function of the individual legumin and albumin determinations. While if affords a ready way of combining the major components of pea seed proteins into one comparative value an important reservation concerning the sulfur index and its use in plant breeding needs to be stated. This is the assumption that there will be no change, quantitatively or qualitatively, in the protein composition of legumin and/or albumin when their proportions are altered genetically.

High legumin high albumin recombinants were only found in the round *R*-F_2 subpopulation, but because sampling procedures were destructive, progeny testing was not possible. This leaves open the question whether these four F_2 seeds were in fact correlation breakers and whether they would breed true for high legumin and high albumin contents, and consequently higher S-amino acid contents. Further studies are needed in this cross and other crosses to confirm the existence of high legumin high albumin recombinants by non-destructive sampling of F_2 seeds and progeny testing, or by assaying F_3 families.

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Announcement

Plant Genetic Engineering Study Sets Timetable for Improvements

A leading seed and plant science consulting firm has recently completed a three-year in-depth study of the impacts of genetic engineering on 28 key crops. Crop and seed value increases for the 10 most important species are detailed, together with a timetable for commercialization.

L. William Teweles & Co. from Milwaukee, Wisconsin conducted more than 400 interviews with agricultural experts, scientists and business persons around the world in reaching the conclusions contained in the 700-page report, The New Plant Genetics.*

The New Plant Genetics is a group of new technologies, principally plant tissue culture and recombinant DNA, applied to improving crop performance. They offer the single greatest potential for nonconventional improvement of crop productivity because it enables scientists to transfer positive traits in one plant to a completely different plant species. The new plant genetics permits the overcoming of barriers that now prohibit crossing two different species. In addition to application of these technologies for quantum leaps in food and fiber productivity, the new plant genetics will make conventional plant breeding more efficient. Rapid methods for selection and testing of improved crop varieties will shorten dramatically the six-to-12-year period now needed by traditional plant breeders to create a new commercial variety.

Seed is still the envelope in which genetic improvements are delivered to the farmer. Without seed, substantial social benefits, revenues and profits from the new plant genetics could not be attained. Conventional plant breeding, seed production and seed marketing practices insure that traits introduced by the new plant genetics are of practical and economic benefit to farmers under actual field conditions.

Improved seed also can be protected legally. "Seed companies perform many major functions in bringing the new plant genetics to the marketplace", commented John Kaiser, Senior Consultant at Teweles. "In addition to testing, multiplying and marketing improved seed, seed companies help set new plant genetic research objectives and provide the commercial interface between the laboratory and the farmer's field."

The new plant genetics is expected to add $ 5.6 billion to the annual value of crops before the year 2000. After 2000, the added crop value from new plant genetics improvements will skyrocket to $ 20 billion annually.

Like crop values, the value of seed will increase dramatically. The annual retail value of all U.S. seed incorporating improvements from the new plant genetics will rise from about $ 8 million in 1985 to $ 6.8 billion by the year 2000. The represents a 57% annually compounded growth rate.

Eighty-five percent of the estimated commercial impact of new plant genetics-improved seed is expected in major crops, in advanced countries. These crops include:

– Wheat	– Corn	– Rice
– Barley	– Sorghum	– Soybeans
– Alfalfa	– Cotton	– Tomato
– Sugarbeet		

These 10 crops represent 80% of annual retail seed consumption value in 11 countries:

– United States	– Canada	– Japan
– Australia	– France	– West Germany
– Denmark	– The Netherlands	– Italy
– Spain	– United Kingdom	

These countries represent 90% of annual retail seed consumption in the developed free world.

While many crop-specific problems are still being researched, some improvements of the new plant genetics are in development now. "Tissue culture is now being used routinely to select for attributes in tomatoes, tobacco, potatoes and sugarcane", said Dr. George Kidd, Teweles' Advanced Science Consultant. "However, more complex modifications in crops such as corn, wheat and cotton await further refinements in recombinant DNA technology. Some modifications will be field tested starting in the late 1980s. The rate of application will vary by crop."

* The report has been written for industrial companies and sells for $ 30,000.00 a copy.
More information: L. William Teweles & Co. 777 East Wisconsin Avenue, Milwaukee, Wisconsin 53202, USA. Tel. (414) 2 73-48 54, Telex 260 311