

## GENETIC ENHANCEMENT OF SOYBEAN

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### ABSTRACT

Soybean is second most important oil seed crop in India. Yellow seeded soybean was introduced in India in 1963-64. Over a period of three decades there has been an exponential increase in area and production of the crop. But the productivity is stagnant around 1 tonne/ha whereas the world average is 2240 kg/ha. In this article an attempt has been made to analyse various reasons for low productivity and some suggestions have been made to increase productivity.

**Key Words :** Genetic enhancement, narrow genetic base, physiological constraints, future prospects

Soybean is a major oil seed crop. It is already contributing to the extent of 10% of the domestic edible oil pool and the country earns valuable foreign exchange to the tune of Rs. 2500 crores through export of soymeal. Thus, the role of soybean as a protein rich food crop or oil-crop is now too well known to be emphasized. If soymeal can be utilized domestically, it can play a very vital role in adequately meeting the acute protein deficiency in our country.

Soybean made its debute in this country in 1963-64 but in a short span of less than three decades, area under soybean cultivation reached to over 60 lakh hectares in 1998-99 from a negligible 0.32 lakh hectares in 1970-71 and production increased to 61 lakh tonnes in 1998-99 from 0.14 lakh tonnes in 1970-71. Productivity almost doubled from 438 kg/ha in 1970-71 to 813 kg/ha in 1973-74 [1]. Since then it is stagnant around 950 kg/ha. The increase in production is due to exponential increase in area (Fig. 1). The world average is 2240 kg/ha and in USA average productivity is around 2618 kg/ha. In terms of productivity India stands at 55<sup>th</sup> position in the world [2].

### *Genetic enhancement programme*

Soybean is not a stranger in the northern hilly areas of India [3] but it is comparatively a new crop to the farmers in the plains. Systematic efforts to grow

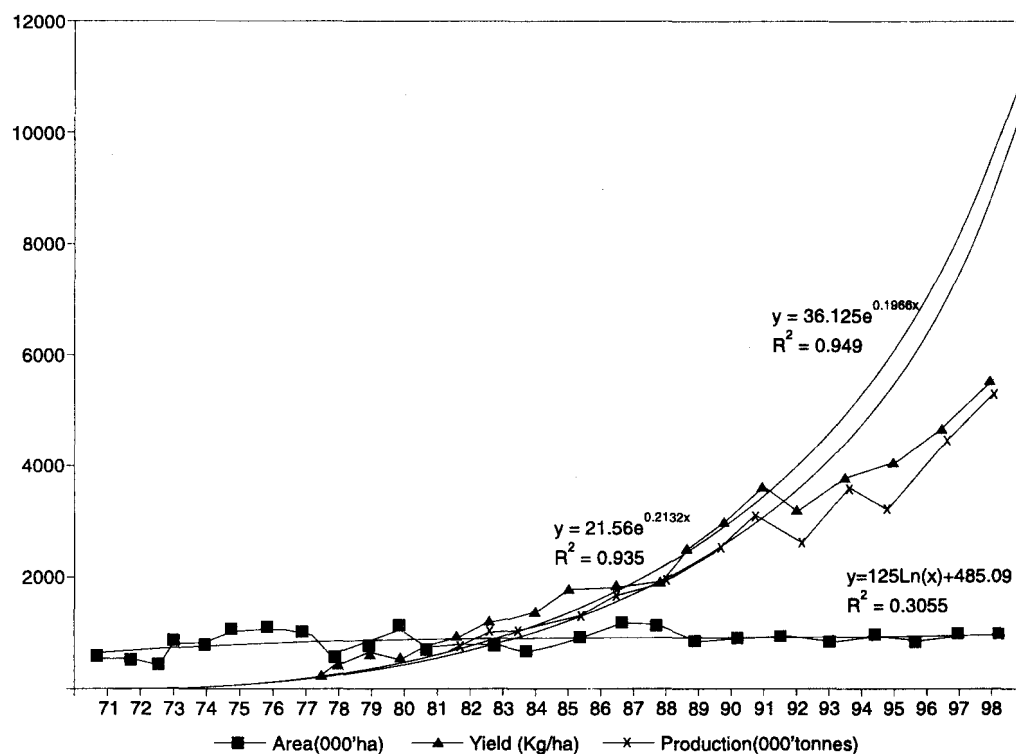


Fig. 1. Trend in area, production and yield of Soybean in India, 1971-98

this crop in the plains during 1965-66 with some US-bred yellow seed varieties yielded promising results. [1]. Encouraged with this success and keeping in mind that a dynamic varietal improvement programme is an absolute necessity to sustain the progress of improvement of any crop, the Indian Council of Agricultural Research started an All India Coordinated Research Project on Soybean Improvement in 1967, IARI, New Delhi as main centre, Pantnagar and Jabalpur as special centres and six sub-centres located in different agroclimatic regions of the country including backward and tribal areas. Since then the project has been working on all aspects of soybean improvement. As a first step about 3500 lines were obtained from USDA and were evaluated at Pantnagar and other centres, and from these introductions, several promising varieties were released for cultivation in India [4] (Table 1). The US-bred varieties were subsequently found to be susceptible to a host of insect pests and diseases. They also suffered from poor germinability under field conditions. The development of high yielding pests and disease resistant varieties with better germination and wide adaptation has therefore, been the main objectives of the

**Table 1. Pedigree/origin of introduced soybean varieties**

Variety	Year of release	Pedigree/origin
Bragg	1969	Introduction from USA
Lee	1969	Introduction from USA
Improved Pelican	1969	Introduction from USA
Hardee	1976	Introduction from USA
Monetta	1985	Introduction from USA
Punjab - 1	1978	Selection from Nanking variety

Source : NRCS Technical Bulletin 2.

breeding work under AICRP on soybean. Since its inception till recent times, the programme has brought out more than 60 high yielding and disease resistant varieties [5]. The programme has many significant achievements to its credit. The most significant has been in the area of breeding varieties with improved storability, germination, resistance to shattering, resistance against biotic stresses and high yield. Significant progress has also been made in developing suitable agronomic package of practices and in the area of pest management and biological nitrogen fixation [6]. To assess the impact of breeding on yield, a three year field experiment was conducted to evaluate forty three soybean varieties developed in the domestic breeding programme of India from 1969 to 1993 [5]. The study divided the varietal development programme into two different classes, namely, those developed as a direct or secondary selection from exotic or indigenous germplasm designated as product of "Selection cycle - 1" and those developed through hybridization as product of "Selection cycle - 2" (Table 2). The study revealed that varieties from Selection cycle - 1 showed four times

**Table 2. Changes in mean seed yield and other agronomic traits of Indian soybean varieties resulting from two consecutive selection cycles**

Trait	Selection cycle-1		Kalitur	Selection cycle-2		Bragg
Yield (kg/ha)	16.53 ±	4.46	4.29	19.60 ±	4.46	22.55
Biomass (Kg/ha)	63.20 ±	11.66	50.65	66.30 ±	11.66	74.75
Harvest index	0.25 ±	0.06	0.07	0.29 ±	0.06	0.30
Maturity (days)	106.0 ±	3.08	115.00	106.0 ±	3.08	105.00
Pods/plant	58.4 ±	18.33	42.40	55.9 ±	18.33	54.30
Height (cm)	85.9 ±	11.89	107.10	79.8 ±	11.89	72.00

Source : [5]

higher seed yield and harvest index as compared to the farm traditional variety 'Kalitur'. The varieties from "Selection cycle - 2" showed 19 per cent higher seed yields and 16 per cent increase in harvest index over Selection cycle - 1. The annual genetic gain in seed yield of soybean varieties released in India from 1969 to 1993 was approximately 22 kg ha<sup>-1</sup>. In this study an indigenous variety 'Kalitur' was used for comparison. However, the comparison would have been more appropriate with 'Bragg' (Table 2). Which is a long term check in AICRP on soybean in all the zones and is in cultivation since 1969. Table 2 shows that there has been no significant gain over 'Bragg'. In fact, we have reached a yield plateau. The data on agronomic trials also supports this view (Table 3). The average yield of improved varieties is

**Table 3. Soybean yield (kg/ha) in front line demonstrations**

Year	Farmers practice	Improved technology
1989-90	901	1951
1990-91	1280	1959
1991-92	1446	1991
1992-93	1427	1933
1993-94	1407	1899
1994-95	1360	1810
1995-96	1385	1839
1996-97	1501	1824
1997-98	1409	1852

Source : Project Coordinators Report 1997-98

stagnant around 2.5 to 3.0 q/ha. Data on 'highest yield', 'best check yield' and 'zonal mean' obtained in initial varietal trial (IVT) under AICRP from 1981 to 1997 is summarized in Tables 4 and 5. In the Northern Hill Zone, in seven out of 16 trials conducted over the years best check is the highest yielder. Similarly in Northern Plains Zone in six trials out of 18 conducted over the years again the best check is the highest yielder. In Central Zone also in seven out of 15 trials conducted over the years best check is either at par or is the highest yielder and in Southern Zone in nine out of 16 trials over the years best check is the highest yielder.

Thus the data of AICRP on soybean shows that we have reached a yield plateau on yield productivity (Tables 4 & 5). The reason appears to be the narrow genetic base of the breeding material being used. The practice by the soybean breeders in

**Table 4. \*Performance of best entry and best check (Kg/ha) along with zonal mean in All India Coordinated Trials on soybean**

Year	Northern hill zone			Northern plain zone		
	Highest yield	Best check	Zonal mean	Highest yield	Best check	Zonal mean
1980	-	-	-	1950	1964	1711
1981	1354	1110	1184	1777	1358	1594
1983	2056	2056	1898	2245	2045	2046
1984	1384	1384	1311	2346	1949	2046
1985	1696	1647	1615	2408	2165	1988
1986	2987	2831	2472	2329	2329	1981
1987	2479	2061	2027	1902	1543	1327
1988	1919	1919	1750	2165	1887	1707
1989	2487	2192	2317	1512	1512	1223
1990	2335	2335	2029	1847	1847	1365
1991	2685	2277	2142	2500	2500	1919
1992	2067	2061	1800	2437	2078	2051
1993	3122	3122	2652	1760	1570	1424
1994	2411	2411	1679	1390	1390	1186
1995	2508	1505	1807	1919	1718	1707
1996	-	-	-	1893	1672	1648
1997	1904	1508	1562	2109	1905	1658

\*Source: Project Coordinators Report; - data not available

India has been to use elite × elite crosses, a dangerous trend barring a few exceptions. This is of great concern, since only a few elite lines which formed the parents in the first cycle of breeding have been the base of the varietal development programme. These lines which formed the parents in the first cycle of breeding are themselves derived from a very narrow genetic base (Table 6). The narrow genetic base of Indian varieties (Table 7) makes them vulnerable to abiotic and biotic stresses. A study to assess the extent of genetic diversity for agronomic traits existing among the 41 elite Indian soybean varieties [7] revealed that about 75 per cent of the varieties fall under two genetically less divergent clusters characterized by a moderate and probably balanced expression of the economically important characters. Since the very same material is being used in crossing programme it offers very little variability to choose from. Hence, there has been no significant increase in genetic

**Table 5. \*Performance of (Kg/ha) best entry, best check and zonal mean in All India Coordinated Trials on soybean**

Year	Central zone			Southern zone		
	Highest yield	Best check	Zonal mean	Highest yield	Best check	Zonal mean
1981	2144	-	1928	2740	2740	2098
1982	2147	2110	2098	2676	2676	2027
1983	2502	2226	2277	3443	2538	2768
1984	1812	1741	1680	2090	1815	1907
1985	2314	2344	2010	1713	-	1656
1986	2219	1933	2000	1792	1792	1558
1987	1971	1971	1781	3338	2943	2998
1988	2578	2350	1948	3242	2724	2826
1989	2147	2110	2098	2676	2676	2027
1990	2639	2048	2175	2226	1814	1713
1991	-	-	-	2927	2927	2520
1992	1958	1861	1772	2332	2276	2098
1993	2383	2383	1727	2511	2495	2294
1994	2545	2381	2047	2372	2340	2110
1995	1998	1998	1752	2214	2025	1984
1996	2221	2078	1996	2102	2102	2018
1997	2001	2001	1774	2340	2231	2054

\*Source: Project Coordinators Report; - data not available

**Table 6. Coefficient of parentage of initial five Introductions of soybean**

Genotype	Lee	CNS	Hardee	Punjab 1
Bragg	0.5000	0.250	0.016	0.060
Lee	-	0.500	0.030	0.125
CNS		-	0.060	0.000
Hardee			-	0.125

yield potential of soybean varieties and yield at research farms have in fact declined in recent years. The pedigree of lines currently under testing in AICRP on soybean confirms the continuation of same elite × elite line crosses (Table 8).

**Table 7. Coefficient of parentage of later developed Indian varieties with respect to initial five introductions of soybean**

S. No.	Indian variety	Coefficient of parentage with respect to
<b>Bragg</b>		
1.	Durga	0.50
2.	VL-Soy-1	1.00
3.	Pusa-37	0.50
4.	Pusa-24	0.50
5.	Pusa-20	0.75
6.	PK-564	0.50
7.	NRC-7	1.00
8.	PK-1042	0.50
9.	MACS-450	0.50
<b>Lee</b>		
1.	Pusa-40	0.50
2.	Pusa-16	0.75
3.	Pusa-20	0.75
4.	JS 71-05	1.00
<b>Improved Pelican</b>		
1.	JS 75-46	0.50
2.	MACS-58	0.50
3.	MACS-124	0.50
4.	MACS-57	0.50
<b>Hardee</b>		
1.	PK-262	0.50
2.	PK-308	0.50
3.	PK-472	0.37
4.	PK-471	0.37
5.	PK-1029	0.25
<b>Punjab-1</b>		
1.	Gujarat Soy-1	1.0
2.	Pusa-22	0.5

**Table 8. Pedigree of lines currently under testing in AICRP on soybean**

S.No.	Line	Pedigree
1.	NRC-37	Gaurav* × Punjab-1*
2.	NRC-38	JS-335* × MACS-58*
3.	NRC-39	PK-308* × NRC-2*
4.	PK-1241	PK-1039 × PK-327*
5.	VLS-50	Bragg* × Anasay
6.	MAUS-49-2	JS 75-46* × JS-80-21*
7.	MAUS-47	Sel. from MACS-308
8.	MACS-716	Sel. from EC 95268
9.	JS-(SH)-92-73	JS-86-79 × JS-71-05*
10.	JS-(SH)-92-46	JS-335* × JS-87-56
11.	HIMSO-1563	Lee* × HIMSO-308

\*Released variety

### *Physiological constraints*

As compared to cereals, soybean has a very low productivity. This is because of physiological constraints. Soybean has a unique seed composition with carbohydrates - 38%, protein - 38%, lipid - 20% and ash 4%. Therefore, soybean not only requires the greatest amount of nitrogen in seed production but is also one of the lowest producers of seed biomass per unit of photosynthates [8]. Protein and lipid which form the major constituent of soybean need almost double the amount of photosynthates required for same amount of carbohydrate, the major constituent of cereals [9].

Biomass productivity (grams of seed per gram of photosynthate) was one of the lowest at 0.50 g/g and nitrogen requirement at 29 mg/g (milligrams of nitrogen/gram of photosynthate) was highest for soybean among 24 different crop species studied [8]. Nitrogen requirement of soybean and pulses were so great that sustained seed growth demands continued nitrogen translocation from vegetative tissues. This translocation must eventually induce senescence in these tissues, restrict the duration of seed-fill period and limit seed yield. As soybean supports symbiotic nitrogen fixation, by increasing the fertilizer application its nitrogen requirements cannot be met [9, 10]. Several studies have shown that foliar application of nitrogen at the time of flowering increases grain yield [11-13].

### *Future prospects*

As compared to world average, productivity of soybean in India is almost half. This is because of two reasons, first is the physiological restriction imposed on the crop by nature and secondly because of erroneous breeding strategy. Any strategy to break the yield barrier needs measures which can address to both the problems.



### *Widening the genetic base*

The narrow genetic base of cultivated varieties of Soybean is of global concern. The genetic base of most soybean varieties grown in USA is also narrow since about 80% of their genepool can be traced to between seven to ten introductions made from the same geographical area [14-16]. Four major components directly influence the amount of annual genetic gain that can be achieved in cultivar development programme [17]. These are :

- i) The degree of genetic variability in the source populations available for selection,
- ii) The size of the selection differential,
- iii) The number of years required for selection cycle, which, represents the interval between parental matings and subsequent remating of selected off-springs, and
- iv) The magnitude of the phenotypic variance which in relation to the genetic variance governs the heritability of the trait selected.

Sufficient genetic diversity for various traits (growth, leaf size and shape, flowering and maturity duration, pubescence, seed size and colour, protein and oil %, etc) is present in the germplasm, it depends how the breeders use these traits efficiently and systematically in breeding programme. Palmer *et al.* [19] have discussed in detail about loss of diversity due to breeding and possible ways to increase diversity.

Simulation studies [18] have shown that the theory of getting segregants with elite  $\times$  elite cross will work only if there is sufficient divergence between the parents. Several methods such as use of mid-parent value, coefficient of parentage, best linear unbiased prediction (BLUP), BLUP with no parental data (BLUP (NP)), BLUP with parental data (BLUP (P)) and recently molecular marker data has been suggested for prediction of cross combinations which can give a population with high mean and high genetic variance [20-23]. Emphasis may be given on newer germplasm. Our own material i.e., IC collections may be used with US bred varieties. Attention should be given on enriching the germplasm by introducing germplasm from oriental countries and also from Argentina and Australia.

Another important aspect is variability in cytoplasm. It is assumed that the expression of a character is mostly through the effect of nuclear genes rather than the cytoplasmic effects. However, the predominance of maternal effects and their differential expression over years suggest that a caution be exercised while planning the order of parents for crossing [24, 25]. On the basis of mitochondrial DNA RFLPs four different types of cytoplasm namely, Lincoln type (Group I), Arksoy type (Group II), Bredford type (Group III) and Soja-forage type (Group IV) have been identified

[26]. Hundred and thirty eight different US bred varieties studied were classified into four different groups. Hill, Lee, Davis, Hardee and Bragg which appear in the pedigree of majority of Indian cultivars were all classified to group III or Bredford type. The variability for cytoplasm may also be low in Indian cultivars though no such study has been carried out till today. Majority of varieties developed at Pantnagar has *Glycine soja* in their pedigree, presence of at least soja-forage type cytoplasm is ensured.

A study involving interaction between different types of cytoplasm and nuclear genes will also be helpful in devising new techniques to break yield barrier.

Use of wild annual as well as perennial *Glycine* species in breeding programme will help in increasing diversity. The wild annual soybean *G. soja* has been used as a parent in crosses with *G. max* and both species have similar genomes. A number of traits of agronomic importance have already been transferred from *G. soja* to *G. max* [27-29].

#### ***Overcoming physiological constraints***

The energy and nitrogen demand at the time of seed filling in soybean is so high that it cannot be met from current photosynthesis, so it remobilises stored photosynthate from leaves. This sets in senescence in the plants and seed filling is affected. To increase yield therefore, one way is to devise means to meet increased energy and nitrogen demands of the plants and second is to reduce actual energy and nitrogen demand/unit of seed mass produced.

Average protein content of Indian varieties is 40 per cent. The protein content of American and Brazilian cultivars is 2-3% less than the Indian Soybean cultivars. This is not a mere coincidence but a well thought out strategy to increase grain yield by reducing nitrogen requirement and also to release the pressure of nitrogen on the plant, thus delaying senescence. By reducing protein and replacing it by carbohydrates, seed yield/gram of photosynthate can be increased. Actual protein availability can be increased by breeding for better amino-acid composition (higher methionine) and elimination of anti-nutritional factors and trypsin inhibitors.

Selection for individual physiological traits like long-juvenile period[30], long seed-filling duration[31], high nitrogen fixing ability[32], evergreen types, high partitioning efficiency[33] will also help in overcoming the physiological restrictions imposed by the nature. Translating it in ideotype concept[34], breeders may select for :

- i) High biomass (long duration or from vegetable type soybean)
- ii) High partitioning efficiency (from early genotypes)
- iii) Long seed-filling period
- iv) High nitrogen fixing ability

- v) Semideterminate/determinate type
- vi) Resistance/tolerance to biotic and abiotic stresses
- vii) Resistance to pod shattering
- viii) Good germinability
- ix) Resistance against field weathering
- x) High methionine content
- xi) Low phytotoxins and no anti-nutritional factors.

However, a complex relationship between all these characters requires crop - modelling studies to reach an optimum level and to develop an ideotype for different agroclimate zones. Therefore, further gain in genetic yield potential will depend upon development of ideotype for each zone and adoption of appropriate breeding strategy.

#### REFERENCES

1. P. S. Bhatnagar and Nawab Ali. 1993. Country report. *In: Proceedings of the Planning workshop for the establishment of the Asian Component of a Global Network on tropical and subtropical soybeans.* RAPA Publications : 1993/6.
2. F. A. O. Production yearbook 1998. Vol. 52. p. 101.
3. P. S. Bhatnagar and S. P. Tiwari. 1990. Soybean varieties of India. NRCS Technical Bulletin No. 2. NRCS (ICAR, Publ.), Khandwa Road, Indore.
4. Hari Har Ram. 1994. Breeding approaches in soybean. *In: Crop Breeding in India.* (ed. H. G. Singh, S. N. Mishra, T. B. Singh and H. H. Ram). pp. 532.
5. P. G. Karmakar and P. S. Bhatnagar. 1996. Genetic Improvement of Soybean varieties in India from 1969 to 1993. *Euphytica.*, 90: 95-103.
6. P. S. Bhatnagar. 1998. Unpublished Project Coordinator's report on AICRP on soybean for 1997-98.
7. P. G. Karmakar, P. S. Bhatnagar, V. S. Bhatia and O. P. Joshi. 1998. Genetic diversity among Indian soybean varieties. *Soybean Genetics Newsletter.*, 25: 74-75
8. T. R. Sinclair and C. T. deWit. 1975. Comparative analysis of photosynthate and nitrogen requirements in the production of seeds of various crops. *Science.*, 189: 565-67.
9. F. W. T. Penning de Vries, *In: Photosynthesis and Productivity in Different Environments* (ed. J. P. Cooper). Cambridge Univ. Press, Cambridge.
10. E. J. Ralston and J. Imsande. 1983. Nodulation of hydroponically grown soybean plants and inhibition of nodule development by nitrate. *J. Exp. Bot.*, 34: 1371.
11. John Streeter. 1988. Inhibition of Legume Nodule formation and N<sub>2</sub> fixation by Nitrate. *C.R.C. Critical Reviews in Plant Science.*, 7: 1-23.
12. V. P. Maini and R. K. Sharma. 1997. The breeding options for increasing soybean productivity. *Annals of Agric. Res.*, 18: 3, 383-84.
13. M. M. Selim. 1997. Effect of sowing methods and foliar application with urea and some micronutrients on growth and yield of soybean (*Glycine max* (L.) Mers). *Egyptian J. of Agronomy.*, 17: 1-2, 141-54.
14. X. Delannay, D. M. Rogers and R. G. Palmer. 1983. Relative genetic contributions among ancestral lines to North American Soybean Cultivars. *Crop Sci.*, 23: 944-49.

15. Z. Gizlice, T. E. Carter Jr and J. W. Burton. 1993. Genetic diversity in North American Soybean. 1. Multivariate analysis of founding stock and relation to coefficient of parentage. *Crop Sci.*, **33**: 614-20.
16. Z. Gizlice, T. E. Carter Jr. and J. W. Burton. 1994. Genetic base for North American public soybean cultivars released between 1947 and 1988. *Crop Sci.*, **34**: 1143-51.
17. W. R. Fehr. 1984. Genetic Contribution to Yield Gains of five major crop plants. *In*: Special publication No. 7. Crop Science Society of America, Madison, Wisconsin. pp. 15-45.
18. R. G. Palmer, T. Hymowitz and R. L. Nelson. 1996. Germplasm Diversity Within Soybean. *In*: Soybean Genetics, Molecular Biology and Biotechnology. (eds. D.P.S. Verma and R. C. Shoemaker), CAB International, Wallingfor, U.K.
19. T. B. Barley and R. C. Comstock. 1976. Linkage and the synthesis of better genotypes in self-fertilizing species. *Crop Sci.*, **16**: 363-70.
20. Henderson. 1975. Best linear unbiased estimation and prediction under a selection model. *Biometrics.*, **31**: 423-77.
21. D. M. Panter and F. L. Allen. 1995. Using best linear unbiased predictions to enhance breeding for yield in soybean : I. Choosing parents. *Crop Sci.*, **35**: 397-405.
22. D. M. Panter and F. L. Allen. 1995. Using best linear unbiased predictions to enhance breeding for yield in soybean : II. Selection of superior crosses from a limited number of yield trials. *Crop Sci.*, **35**: 405-410.
23. J. F. F. Toledo. 1992. Mid parent and coefficient of parentage as predictions for screening among single crosses for their inbreeding potential. *Rev. Brasil. Genet.*, **15**: 429-37.
24. M. Lee. 1995. DNA markers and plant breeding programs. *Adv. Agron.*, **55**: 265-344.
25. S. De Brown, R. Miller, D. E. Green and R. C. Shoemaker. 1990. Effect of unique cytoplasm on agronomic and physiological traits of soybean. *In*: D. Bledie (ed.) Proceedings of 3rd Biennial Conf. Mol. Cell Biol. of Soybean. Iowa State University, Ames, Iowa, p8.
26. J. Dayde. 1989. The possible influence of cytoplasm on the performance of reciprocal soybean hybrids. *Euphytica.*, **44**: 1-2, 49-53.
27. E. A. Grabau, W. H. Davis, N. D. Phelps and B. G. Gengebach. 1992. Classification of soybean cultivars based on mitochondrial DNA restriction fragment length polymorphisms. *Crop Sci.*, **32**: 271-74.
28. J. C. Thorne and W. R. Fehr. 1970. Incorporation of high-protein, exotic germplasm into soybean population by 2 and 3 - way crosses. *Crop Sci.*, **10**: 652-55.
29. J. C. Thorne and W. R. Fehr. 1970. Exotic germplasm for yield improvement in 2 - way and 3 - way soybean crosses. *Crop Sci.*, **10**: 677-78.
30. R. A. Kiihl and A. Garcia. 1989. The use of long-juvenile trait in breeding soybean cultivars. *In*: (eds. A. J. Pascale). Proc. World Soybean Res. Conf. IV. AASOJA, Aires, pp. 994-1000.
31. A. S. Vasilas, R. L. Nelson, J. J. Fuhrmann and T. A. Evans. 1995. Relationship of Nitrogen utilization patterns with soybean yield and seed fill period. *Crop Sci.*, **35**: 809-813.
32. B. L. Dreyfus, H. G. Diem and Y. R. Dommergues. 1988. Future directions for biological nitrogen fixation research. *Plant and Soil.*, **108**: 191-199.
33. F. W. Synder and G. E. Garlson. 1984. Selecting for partitioning of photosynthetic products in crops. *Adv. Agron.*, **36**: 47-72.
34. C. M. Donald. 1968. The breeding of crop ideotypes. *Euphytica.*, **17**: 385-403.