

Yield Improvement in Soybeans Using Recurrent Selection

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Abstract

The objective of this study was to evaluate the potential of recurrent selection for improving seed yield in a soybean population. Seventeen parents, chosen for their high yield potential in the sub-tropical environments of Southern and Central Queensland were intermated using a diallel cross mating system. F₁ plants were intercrossed in pairs for two more generations and then allowed to self for two generations to produce the base population. The selection criterion was the seed yield of S₁ lines grown at Hermitage Research Station. The selection intensity was approximately 10%. After five cycles of recurrent selection the mean yield of the population and the mean yield of the lines selected for recombination had improved by 17% and 54% respectively, in comparison with one of the original parents, Davis.

Progress from recurrent selection was evaluated using fifty randomly selected lines from the base population and from each of the first three cycles of selection. The average gain per cycle in seed yield, averaged over five sites was 128 kg ha⁻¹ or 5.4% of the yield of the base population. Greater progress (9.8% per cycle) was measured at the testing site for selection (Hermitage Research Station) which was heavily infested with phytophthora root and stem rot than at three other sites (2.7% per cycle) which has nil or low levels of disease.

Broad sense heritabilities for the base population and for cycles 1, 2 and 3 in the evaluation trial were 0.34, 0.25, 0.13 and 0.14 respectively compared with a mean heritability of 0.64 for the first five cycles of the selection experiment. Expected gain from further cycles of selection was estimated at 102 kg ha⁻¹ per cycle for three replicates at a single site.

In the evaluation trial correlated responses to selection for yield were found in a number of other traits. Days to flowering was reduced by 0.8 days/cycle while days to maturity increased by 1 day/cycle. Seed shattering score was significantly reduced from 0.98 to 0.69 while there were only minor changes in plant height, lodging and seed coat quality score. Resistance to root and stem rot and seed coat mottling, due to primarily to soybean mosaic virus, were also significantly increased. The improvement in phytophthora resistance was expected as the field used for S₁ yield testing had become infested with the disease. A covariate analysis indicated that about half the improvement in seed yield at the Hermitage site was due to the correlated response of increased resistance to phytophthora root and stem rot.

Keywords: soybeans, recurrent selection, phytophthora resistance, yield.

Introduction

The classical approach in breeding for yield in self-pollinated species is to cross two superior parents and then develop homozygous lines by allowing the progeny to self for a number of generations. Superior lines are then identified by yield

testing and used as new cultivars and possibly as parents of new crosses. The weakness of this approach is that a limited gene pool is used for each cross, cycle times are very long (5–10 years) and yield increases per year may be quite small.

Plant breeders have developed a number of different breeding systems to try to enhance breeding progress. Recurrent selection in a diverse population utilising single plants or first selfing generation (S_1) testing has the advantage of reducing cycle time. Gardner (1977) has been successful in using this method for more than fifteen cycles of selection in maize to improve seed yield. Kenworthy and Brim (1979), obtained a yield increase of 134 kg ha^{-1} per cycle when selecting for yield *per se* in soybeans in North Carolina. Sumarno and Fehr (1982) obtained yield responses of 120, 24 and -14 kg ha^{-1} per cycle in early, midseason and late maturity soybean populations in Iowa. Hanson *et al.* (1967) have discussed the theoretical advantages of using recurrent selection in self-pollinated species.

Materials and Methods

A study was undertaken to evaluate the potential of recurrent selection for increasing the seed yield in a soybean population. The base population (C_0) for this study was created by intercrossing seventeen lines in a diallel cross mating system (Table 1). The lines were chosen to represent diverse geographic regions while at the same time possessing high yield potential. A wide range of maturity groups were represented so that it would be possible to extract genotypes adapted to tropical and subtropical environments. Some of the lines were also resistant to phytophthora root and stem rot, caused by *Phytophthora megasperma* Drechs f. sp. *glycinea* Kuan & Erwin and/or rust caused by *Phakopsora pachyrhizi* Syd. R P Syd. Phytophthora root and stem rot is widespread in the soybean growing areas of southern Queensland (Rose *et al.* 1982) and although it caused serious losses in the early 1980's, the disease has been far less severe in recent years due to the use of field-resistant cultivars. Rust often develops on soybean plants near the end of the growing season (March, early April), but usually does not cause serious losses.

Table 1. Origin and special attributes of seventeen parents which were included in the diallel cross mating system

Parent	Origin	Special attributes
Davis	Arkansas, USA	High yield, resistant to Phytophthora
Flegler	Queensland	High yield
Canapolis	Brazil	High yield, late maturity
BK 1445	Bragg×Daintree	High yield, later maturity
P 24	Bragg×Ogden	High yield
Williams	Missouri, USA	High yield, very early maturity
Chung Hsien No 2	Taiwan	Vigorous winter growth, resistant to Phytophthora
Taichung 4	Taiwan	Resistant to rust and Phytophthora
P.I. 200492	Taiwan	Resistant to rust and Phytophthora
E.G.I.	Philippines	Late maturity, indeterminate
Aki Sengokku	Japan	Large seed, resistant to Phytophthora
U.F.V. 72-1	Brazil	Late maturity
70/39	Zimbabwe	High yield, indeterminate
65-2-6-3-B1	Hill×Lee	Early maturity, high yield
SH 1188	Semstar×Hill	Early maturity, high yield
Fitzroy	Semstar×Wills	High yield
HS 1421	Hinn×Semmes	High yield

The diallel cross resulted in 136 different F_1 's which were intercrossed in pairs to make 68 four-way crosses and again intercrossed to make 34 eight-way crosses. 108 F_1 plants from the last series of crosses were then allowed to self-pollinate for two generations. The second generation of approximately 4000 plants became the base population for the recurrent selection program. Progeny of 582 of these plants (S_2 lines) were yield tested in the first cycle. S_1 lines were used in subsequent cycles.

Each cycle of selection consisted of three plant generations. The first was a yield test at Hermitage Research Station near Warwick, Queensland ($28^\circ 10' S.$, $152^\circ 06' E.$). The highest yielding lines were intermated in the next generation and F_1 plants grown out to produce S_1 seed in the third generation. Intercrossing took place in growth chambers during the winter to allow each cycle of selection to be completed in two years.

The sole criterion for selection was seed yield, which was evaluated in a completely randomised design using 5 m single row plots for the first cycle in 1981 and 2 m single row plots in subsequent cycles. Row spacing was 70 cm. Each trial was augmented with check plots of Davis replicated about twenty times. The trial area was flood irrigated when accumulated pan evaporation approximated 90 mm.

A selection intensity of approximately ten per cent was used in each cycle. Selected lines were planted in growth chambers using 12 h photoperiods which synchronised flowering to within a few days. Temperatures were 28 to 30°C during the day and 20 to 24°C during the night, while humidity was kept high on most occasions. These conditions promoted pollen production and fertilisation.

Random mating was practised by collecting equal numbers of flowers each morning from lines to be used as males and attempting to produce an equal number of crossed seed on each female line. On subsequent days different groups of lines were chosen to be female or male lines so that each line made an approximately equal genetic contribution to the next generation. Although no attempt was made to record the male parent of each cross, approximately one third of all possible biparental crosses were successful.

The genetic gain from recurrent selection was evaluated using 50 randomly selected F_4 derived lines from the base population and F_3 derived lines from each of the first three cycles of selection. Three replicates were grown at Hermitage in 1986 and seed harvested from this trial used to plant two replicates at Hermitage, St. George, Kingaroy and Boonah, Queensland in 1987. Randomised complete block designs were used in all cases. The structure of the analysis of variance table and the expected mean squares for this experiment are shown in Table 2. Response to selection was estimated by the linear regression of seed yield on cycle number.

Additional data collected at two or more sites included days from planting to flowering (50% plants with opened flowers), days from planting to maturity (95% of pods brown), plant height, (mean of five plants), lodging scored on a scale from 1 = plants erect to 5 = plants prostrate, shattering scored on a scale from 0 = no shattering through 2 = 10% pods opened to 5 = 100% pods opened. Phytophthora incidence was assessed on a scale where 1 = no disease, 2 = <5% plants infected and 10 = 100% plants infected. Seedcoat quality was scored on a scale from 1 = excellent to 10 = very poor and seedcoat mottling scored on a scale from 1 = no mottling to 10 = 100% mottling.

Gene frequencies for loci controlling flower colour (W_1), pubescence colour (T) and indeterminance (Dt_1) were estimated at Hermitage in 1986 and 1987 by scoring each plot, homozygous recessive, heterozygous or homozygous dominant for each locus and then calculating a mean value for each cycle of selection.

Variance components from the analysis of variance for each cycle of selection and from the across site evaluation trial were used to estimate appropriate genotypic variances (σ^2_g). Phenotypic variance (σ^2_p) for the testing generations of each selection cycle was calculated using the formula:

$$\sigma^2_p = \sigma^2_g + \sigma^2_e/r,$$

where σ^2_e = error mean square and r = number of replicates.

Phenotypic variance for the across site evaluation trial was calculated using the variance components from Table 2:

$$\sigma_p^2 = \sigma_{l:c}^2 + \sigma_{sl:c/s}^2 + \sigma_e^2/rs,$$

where s = number of sites and r = number of replicates.

Heritability (h^2) and expected genetic advance from selection (Δ) for each of the cycles (C_0 , C_1 , C_2 and C_3) were calculated from the variance components in Table 2 using the formulae:

$$h^2 = \sigma_g^2/\sigma_p^2 \text{ and } \Delta = kh^2\sigma_p,$$

where k = selection differential expressed as a multiple of the phenotypic standard deviation. Ten percent selection ($k = 1.76$) was used throughout.

Table 2. Structure of analysis of variance table and expect mean squares for evaluation trial grown at five sites

Source	d.f.	Expected mean squares
Sites	4	$\sigma_e^2 + \sigma_{sl:c}^2 + 200\sigma_s^2$
Cycles	3	$\sigma_e^2 + \sigma_{sl:c}^2 + 50\sigma_{sc}^2 + 5\sigma_{l:c}^2 + 250\sigma_c^2$
Sites \times cycles	12	$\sigma_e^2 + \sigma_{sl:c}^2 + 50\sigma_{sc}^2$
Lines in cycles	196	$\sigma_e^2 + \sigma_{sl:c}^2 + 50\sigma_{l:c}^2$
Sites \times lines in cycles	784	$\sigma_e^2 + \sigma_{sl:c}^2$
Pooled error	1042	σ_e^2

Results and Discussion

The mean yield of S_1 lines, mean yield of selections, and the estimates of heritability for five cycles of selection for seed yield are shown in Table 3. The lines tested in the first cycle particularly, showed a very wide range in yield. Many of the low yielding lines suffered from seed shattering, lodging or susceptibility to phytophthora root and stem rot. Fortunately, some of the parents used in this study are resistant to this disease (Table 1) even though the parents were selected and crossing initiated before the disease was recognised as being a serious problem in Queensland (Pegg *et al.* 1980). The experimental area used in 1981 for growing the yield test in C_1 was found to be badly infested with *P. megasperma* f. sp. *glycinea* and was also used for the yield test in later cycles of selection.

Table 3. Test population size, number of lines selected, mean yields of populations, selections and check variety Davis and estimates of heritability for the first five cycles of recurrent selection at Hermitage Research Station

Year of test	Cycle No.:	1	2	3	4	5
		1981	1983	1985	1987	1989
Population size		582	518	337	444	438
Number selected		61	52	34	44	44
Mean yield (kg ha ⁻¹)		2938	2081	2606	3693	2589
Mean yield of selections (kg ha ⁻¹)		3812	3159	3461	4863	4080
Mean yield of Davis (kg ha ⁻¹)		3059	2424	2604	3593	2280
Heritability		0.73	0.54	0.62	0.58	0.71

The mean yield of all the lines tested and the mean yield of the selected lines increased by 17% and 54% respectively after five cycles of selection in comparison with the check variety Davis (Table 3). The heritability estimates which had a mean value of 0.64 for five cycles are inflated by the large genetic variation for yield in the base population and by the effect of segregation for phytophthora root and stem rot resistance and seed shattering. The genotype \times environment interaction was also minimised as trials were grown at the same site and there is the possibility that genotypes which were specifically adapted to this site were selected. Mice damage to late maturing lines during the seed filling period occurred in 1989 in the C₅ yield trial which meant selection probably favoured early maturing lines which normally would be lower yielding. The increased number of poorer yielding lines would have increased genetic variance for seed yield and thus inflated the heritability estimate. The heritability estimates indicate that substantial gains can be made by selecting for seed yield in this population even allowing for the fact that the estimates are somewhat inflated. There is a good possibility of developing cultivars that are much higher yielding than the check variety, Davis which has been widely grown in Queensland since 1975.

The analysis of variance for seed yield of 50 random lines from the base population and from each of the first three cycles of selection, grown at five sites, found that the main effect of cycle of selection was significant at the 1% level as were the lines within cycles (Table 4). The interactions of sites \times cycles and sites \times lines within cycles were also significant at the 1% level. Using linear regression analyses, we found an average yield increase of 128 kg ha⁻¹ or 5.4% per cycle when averaged over the five sites (Table 5). Kenworthy and Brim (1979) achieved a similar result of 134 kg ha⁻¹ or 5.3% per cycle for S₁ selection at one location with 2 replicates. Sumarno and Fehr (1982) realised 120 kg ha⁻¹ or 2.1% per cycle in an early maturing population using F₄ selection. The average yield improvement at the Hermitage site (9.8% per cycle) was greater than at the other three sites (2.7% per cycle). The better response to selection at Hermitage could be expected because Hermitage was used as the S₁ line testing site and because phytophthora root and stem rot was present in both the testing and evaluation sites. Rose *et al.* (1982) and Ryley *et al.* (1989) have shown that there is a highly significant negative correlation between disease incidence and seed yield. There were only low levels or no disease at the other three sites so more resistant lines would not have an inherent yield advantage.

The yield increase from one cycle to the next was non-linear. The largest increase in yield was achieved during the first cycle of selection while the increase from C₁ to C₂ was not significant. Selection in the first cycle particularly, was partly a selection against traits such as susceptibility to phytophthora root and stem rot and seed shattering which would have a large depressing effect on seed yield itself. Assuming a few genes of large effect associated with these traits, large improvements in seed yield in the first one or two cycles would be expected.

Variance component estimates for the main effects and interactions are shown in Table 4. Genotypic and genotype \times environment effects for each cycle were also estimated. The highly significant mean squares for lines within cycles suggests that the population is highly variable and offers good prospects for further yield increases. When this variance is partitioned for each cycle of selection the estimates of genotypic variance for C₀ and C₁ are much greater than for C₂

Table 4. Mean squares and variance component estimates for cycles 0 to 3 in the evaluation trial grown at five sites*, ** significance at the 5% and 1% probability levels respectively. Mean squares were multiplied by 10^{-3}

Source	d.f.	Mean squares	Variance component
Sites	4	173924**	868351
Cycles	3	7879**	25545
Sites×Cycles	12	1176**	18444
Lines in Cycles	196	562**	61598
Lines in Cycle 0	49	847**	113204
Lines in Cycle 1	49	746**	86461
Lines in Cycle 2	49	329*	22904
Lines in Cycle 3	49	325*	23824
Sites×Lines in Cycles	784	254**	164292
Sites×Lines in Cycle 0	196	281**	191932
Sites×Lines in Cycle 1	196	314**	224122
Sites×Lines in Cycle 2	196	215**	125261
Sites×Lines in Cycle 3	196	235**	115855
Pooled error	1042	90	89522

and C_3 , again suggesting that many of the poorer yielding and phytophthora susceptible genotypes were eliminated in the first two cycles of selection.

The mean squares for sites×lines within cycles were also highly significant with variance components that were considerably larger than those associated with the mean squares for lines within cycles. This genotype×environment interaction is at least partially explained by the different response of phytophthora resistant and susceptible lines at sites other than Hermitage. When this is partitioned for each cycle, the mean squares for C_1 and C_2 are again considerably larger than for C_2 and C_3 . The heritability estimates for C_2 and C_3 were 0.13 and 0.14 respectively compared with 0.34 and 0.25 for the base population and C_1 . However, these values are still high enough that selection will still be effective.

Table 5. Mean yield (kg ha^{-1}) at five sites of 50 randomly selected lines for three cycles of recurrent selection

	Hermitage 1986	Hermitage 1987	St. George 1987	Boonah 1987	Kingaroy 1987	Mean
C_0	2029	3253	1950	3381	1282	2379
C_1	2408	3494	2194	3608	1452	2631
C_2	2506	3707	2258	3417	1388	2655
C_3	2958	3769	2154	3711	1400	2789
Davis	2643	3221	2327	3988	1266	2689
l.s.d. ($P = 0.05$)	124	113	74	188	65	53
Gain/cycle	289	176	68	80	29	128

While the strategy of selecting at a single site was effective in achieving substantial realised gains in yield in the first three cycles of selection (128 kg ha^{-1}), the expected gain for subsequent cycles using three replicates at one site is reduced to 102 kg ha^{-1} if we use the lower values for heritability and phenotypic

variance estimated for C_2 . A significant improvement to 139 kg ha^{-1} in expected gain from selection can be achieved by using three sites with one replicate at each site. This alternative selection strategy uses the same number of plots, but would be more costly to operate. However the improvement in selection efficiency should be well worth the extra cost.

The effects of selection for yield on the physiological characters, days to flowering and maturity are shown in Table 6. There was a significant reduction in days to flowering for C_2 and C_3 which contrasted with a significant increase in maturity at each site resulting in a mean increase in maturity of about 1 day/cycle of selection. Apparently selection for yield has reduced days to flowering and increased the length of the pod filling period. This selection for delayed maturity could be partly due to border effects in unbordered plots which would favour later maturing lines.

Table 6. Mean days to flowering and maturity of 50 randomly selected lines for three cycles of selection for yield

	Days to flowering				Days to maturity			
	Hermitage 1986	Hermitage 1987	Kingaroy 1987	Mean	Hermitage 1986	Hermitage 1987	Kingaroy 1987	Mean
C_0	73.4	64.3	55.1	63.2	114.9	140.1	120.2	135.1
C_1	73.9	63.6	54.1	63.9	147.3	141.1	122.1	136.8
C_2	67.8	59.7	50.9	59.4	148.6	138.2	121.8	136.2
C_3	70.0	60.5	52.2	60.9	149.2	142.6	122.6	138.1
l.s.d. ($P = 0.05$)	0.6	0.6	0.4	0.3	0.9	0.7	0.9	0.5

Table 7. Effect of three cycles of selection for yield on plant height and lodging score
Plant height is mean of 5 plants from each line at maturity. Lodging scored on a scale 1 = no lodging, 5 = plants prostrate

	Plant height (cm)				Lodging score				
	Hermitage 1986	Hermitage 1987	Kingaroy 1987	Mean	Hermitage 1986	Hermitage 1987	St. George 1987	Kingaroy 1987	Mean
C_0	74.7	102.3	76.1	84.4	2.2	1.9	2.1	2.5	2.2
C_1	78.0	103.5	75.0	85.5	2.2	2.3	2.2	1.9	2.2
C_2	74.9	95.4	70.7	80.3	1.9	1.9	1.6	2.2	1.9
C_3	80.6	100.5	74.0	88.0	2.2	2.3	1.8	2.3	2.2
l.s.d. ($P = 0.05$)	1.5	1.8	1.8	1.0	0.1	0.1	0.1	0.1	0.07

Plant height was measured at three sites (Table 7). There was a significant reduction in height between cycles one and two but most of this change was negated in cycle 3. This effect occurred at all three sites and mean differences were significant. This could be associated with the selection of later maturing lines which tend to be taller. Lodging was measured at four sites (Table 7). There was an improvement in lodging score from C_1 to C_2 which was again reversed in the next cycle. This effect was reflected in the mean scores for each cycle and was highly significant. Similarly, this could be associated with the selection of later maturing lines found in unbordered plots which would tend to be taller and

more lodging susceptible. Sumarno and Fehr (1982) found significant increases in maturity, plant height and lodging score in some but not all populations.

Seed shattering was measured at four sites (Table 8). There was a large improvement in shattering from C_0 to C_1 at the two sites, Hermitage 1986 and St. George where shattering was quite severe in some lines. The effect was smaller at the other sites as conditions were not suitable for shattering. Harvested seed yield is usually seriously reduced in lines which are prone to shattering.

Table 8. Effect of three cycles of selection for yield on seed shattering score and phytophthora root and stem rot score

Shattering score = mean of 50 lines. Each row rated on a 0-5 scale 0 = no pods open, 2 = 10% pods open, 5 = 100% pods open. Phytophthora score = mean of 50 lines. Each row rated on a 1-10 scale. 1 = no disease, 2 = 5% plants infected, 5 = 20% plants infected, 7 = 50% plants infected, 1-10 = 100% plants infected

	Hermitage		Shattering score			Phytophthora score		
	1986	1987	St. George 1987	Kingaroy 1987	Mean	Hermitage 1986	1987	Mean
C_0	1.07	0.46	2.02	0.36	0.98	3.05	2.20	2.62
C_1	0.76	0.50	1.27	0.41	0.74	2.60	1.97	2.29
C_2	0.77	0.43	1.25	0.17	0.66	2.20	2.78	1.99
C_3	0.68	0.47	1.24	0.37	0.69	1.79	1.95	1.87
<i>l.s.d.</i> ($P = 0.05$)	0.15	0.14	0.18	0.16	0.08	0.22	0.29	0.19

Phytophthora rot and stem rot was present in both years at Hermitage. Several lines from the base population were seriously affected and gave very low yields. The most susceptible lines were obviously selected against in the first two cycles of selection and there was consequently a very significant improvement in resistance with each cycle of selection. (Table 8). There was a strong positive correlation between seed yield and resistance to phytophthora at the two Hermitage sites (0.79 in 1986 and 0.34 in 1987), suggesting that about half the improvement in yield during the early cycles of selection could be attributed to an improvement in resistance to the disease. A covariate analysis of the two Hermitage sites using phytophthora ratings as the covariate also supported this conclusion.

These results suggest that substantial improvement in resistance to phytophthora root and stem rot can be achieved while selecting for yield per se. This would be the best method to use for S_1 and S_2 lines or any material which is still segregating. Field scoring for resistance in this material is difficult because Ryley *et al.* (1989) found only a proportion of plants show symptoms of the disease in the field and that substantial yield losses can occur with little evidence of visual symptoms of the disease in some genotypes. Field scoring and laboratory tests (Irwin and Langdon 1982) should be reserved for testing the resistance of elite lines extracted from a population after several cycles of selection.

There was very little change in the scores for seed quality from one cycle to the next at all sites and the overall means for each cycle were generally not significant. However there was a significant improvement in the rating for seedcoat mottling at Hermitage in both years and at St. George while there was no change at Boonah and Kingaroy (Table 9). The overall means were also significant. The seedcoat mottling consisted of streaks (the same colour as the hilum) extending for various distances from the hilum down the seed coat

(Kennedy and Cooper 1967). Such symptoms are typical of soybean mosaic virus which is likely to depress seed yield (Demski and Kuhn 1989).

Table 9. Effect of three cycles of selection for yield on seedcoat mottling score
Visual assessment of seeds using a 1-10 scale. 1 = no mottling, 10 = 100% seeds mottled

	Hermitage		St. George	Boonah	Kingaroy	Mean
	1986	1987	1987	1987	1987	
C ₀	2.47	3.89	1.35	3.04	2.11	2.59
C ₁	1.74	3.23	1.06	3.03	1.97	2.20
C ₂	1.62	3.29	1.09	2.94	2.07	2.20
C ₃	1.60	2.96	1.05	2.91	1.94	2.09
<i>l.s.d.</i> ($P = 0.05$)	0.20	0.29	0.09	0.29	0.16	0.10

The gene frequencies for the loci controlling flower colour (W_1), pubescence colour (T) and indeterminance (Dt_1) shown in Table 10 indicate that there has been a shift in the gene frequency at these loci even though we would not expect that these genes would be strongly linked with genes controlling yield characters. The results indicate a significant shift towards the recessive alleles for white flowers, grey pubescence and determinate habit. The strongest shift from indeterminate to determinant growth habit may indicate that determinance is more desirable in a largely irrigated crop in a sub tropical environment. Determinance is usually associated with reduced lodging and more concentrated flowering and pod filling periods.

Table 10. Effect of three cycles of selection for yield on gene frequencies for flower colour, pubescence colour and indeterminance at Hermitage in 1986 and 1987

	Flower colour (W_1)			Pubescence colour (T)			Indeterminance (Dt_1)		
	1986	1987	Mean	1986	1987	Mean	1986	1987	Mean
C ₀	0.79	0.82	0.81	0.62	0.56	0.59	0.33	0.47	0.40
C ₁	0.79	0.73	0.76	0.42	0.34	0.38	0.38	0.54	0.46
C ₂	0.76	0.74	0.75	0.42	0.42	0.42	0.20	0.23	0.22
C ₃	0.72	0.70	0.71	0.42	0.42	0.42	0.25	0.24	0.25
<i>l.s.d.</i> ($P = 0.05$)	0.04	0.03	0.03	0.03	0.03	0.02	0.06	0.05	0.04

Another explanation may be that the long term selection pressure for high yielding determinate (Dt_1) types in southern China and subsequently southern U.S.A., has resulted in selection of a genetic background that favours the determinate trait in genetic material adapted to subtropical environments. Although we intercrossed for three generations in an attempt to break up linkage blocks before commencing the first cycle of selection, the changes in gene frequency at these three loci may also indicate that blocks of genes are being selected for as a single unit and that by chance genes that are promoting high yield in the selection environment are linked in gene blocks with the alleles for white flowers and grey pubescence. Theoretical evidence has been presented by Hanson (1959) to show that linkage blocks will remain intact in selection experiments of this type.

Conclusion

This study has shown that satisfactory progress for seed yield can be made using recurrent selection in a soybean population. The results achieved are comparable with those achieved with cross-pollinated crops such as maize and indicate that the method could be used with other self-pollinated crops.

The advantages of using recurrent selection are that each cycle of selection is completed in two years and the best lines are being recombined as soon as they have been identified. In more conventional breeding programs, it takes several years to identify and yield test elite lines and it may be eight or ten years before they are used as parents for the next cycle of selection.

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