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The Role of Heterosis in Crop Breeding with Special Reference to Hybrid Cottons

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Introduction: The manifestations of increased size, vigour of development, productivity and similar beneficial effects have long been recognised in many first generation hybrids of plants and animals. This increase in size and vigour resulting from hybridisation has been designated variously as the "stimulating effects of hybridity", "heterozygosis" or "hybrid vigour" and Shull (1914) first proposed the use of the term "heterosis" to denote such a phenomenon. "Heterosis" attracted the early attention of the plant breeders through its conspicuous effects on several economic characters of the crop plants studied, notably that of grain yields in maize (*Zea Mays.* L) a crop taken up for pioneer investigations by the American geneticists.

With the advent of Mendelism after 1900, the subject of heterosis evoked considerable academic interest and the advancement of genetical knowledge provided practical applications The years that followed witnessed remarkable progress in the study of quantitative inheritance and applied genetics. In maize breeding in the United States of America, harnessing of heterosis became the main consideration and the achievements gradually revolutionised corn production and made economic history.

The phenomenal success of hybrid maize inspired extensive work on a variety of plants and valuable contributions to both the academic and utilitarian aspects of heterosis have been made during the last forty years. Informative reviews on different aspects of this subject have appeared from time to time, especially those of East and Jones (1919) in their book on Inbreeding and Outbreeding, East (1936), Ashby (1937. a), Whaley (1944), Ashton (1946) and Ashby (1948).

Theoretical Considerations: The phenomenon of heterosis has been recognised as but another phase of quantitative inheritance and the conception of its manifestations is based on the effects of dominance. Fisher, Immer and Tedin (1932) have even referred to this feature of "transgression" as "superdominance". Genetical and physiological researches on the theoretical aspects of the problem have contributed to the following fundamental concepts as the underlying causes of heterosis. A physiological stimulus arising from heterozygosity (Shull 1908, 1911, and East 1908); dominance of linked favourable genes (Jones 1917); cumulative interaction of divergent multiple alleles of non-defective size-determining genes (East, 1936); and monoheterozygote vigour due to gene pleiotropy (Jones 1945, Gustaffson 1946, 1947, and Granhall 1946) have all been advanced as one or other of the genetic mechanisms responsible for heterosis. A physiological school (Ashby 1930, 1932, 1937. b and Luckwill 1937) has also contributed data to show that size

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Note: Ramasastrulu Munagala Prize Essay 1951.

heterosis in certain maize and tomato hybrids was nothing more than the maintenance of an "initial advantage" in embryo size. Luckwill (1937) further discussing the question of heterosis in embryo size which conferred this "initial advantage" pointed out, that this in turn might be due to stimulus in the heterozygous zygote or other genetic mechanisms. As both size characters and developmental processes are gene controlled, heterosis may be interpreted as due to the cumulative effect of favourable heredity from both the parents.

Manifestations of Heterosis: The ultimate manifestations of heterosis in the different plants would appear to be determined by their inherent growth habit. Heterosis need not be expressed in all plant characters in a given cross. It varies widely in the different species of plants and between crosses in the same species also. It may be exhibited as increase in height, more profuse branching, larger or greater number of leaves, increased number of flowers, heavier yield of seed or fruit, increased weight of plant, hastening of maturity, higher resistance to diseases and insect attack etc. (Ashby, 1948). It is the agricultural utility of several of these characters that has stimulated the use of heterosis in the breeding of crops.

Practical Applications: The commercial utilisation of the phenomenon for crop improvement is known to depend on several factors like the breeding mechanism of the plant, expression of heterosis in economic characters and facility of large-scale seed production. By virtue of these features, hybrid maize remains the outstanding example of achievement in this field of applied genetics. Scientific breeding in maize started first on orthodox lines of selection within self-fertilised lines. The ear-to-row selection as outlined by Shull (1909) was the method in vogue. It was realised that inbreeding in this highly cross-fertilised organism resulted in a loss of vigour and productivity due to the accumulation of unfavourable recessives in the homozygous condition. On the other hand, hybridisation between inbred lines was found, not only to increase the yields appreciably, but combine other desirable effects as well. The edifice of present day breeding methods in maize, is built up on this fundamental fact, and they follow in all essentials one or other of the following methods; viz. (1) the production of single crosses between inbred lines (Shull 1908, 1909); (2) Synthesis of double crosses between different F1 hybrids (Jones, 1918); (3) convergent improvement through a system of backcrossing (Richey, 1927); and (4) multiple convergence utilising different non-recurrent parents for backcrossing (Richey, 1946. b)

There have been improvements in the methods for determining better stocks as foundation, whether inbred or hybrids and in other details as well. Combining ability of parents has been recognised as a specific heritable character (Hay's and Johnson, 1939) and the knowledge utilised in hybridisation. The practical application of these methods has revolutionized maize production in the United States of America which produced some two billion bushels more corn during 1941—'44 on account of the use of hybrid seeds over 65 per cent of the United States maize acreage (Richey 1946 a) which approximates 90.8 million acres (Pal and Ramanujam 1946).

It is also reported that besides maize, first generation hybrids of tomato (*Lycopersicum spp.* Hill) and tobacco (*Nicotiana* spp. L.) are grown to-day on a commercial scale in America and Russia (Ashby 1948). Heterotic effects in yield of fruits, earliness of maturity, and disease resistance in the tomato, and yield and quality of leaves in the tobacco, combined with the advantage of large number of seeds produced in a fruit, render the commercial utilisation of heterosis practicable, in these cases.

In India, recent researches in Madras have resulted in notable success for hybrid *Cumbu* (*Pennisetum typhoides Stapf et Hub*) as a practical proposition. (Rao, Nambiar and Menon, 1951). Two hybrid strains recording over 40 per cent increase in yields over the local variety have been found suitable for cultivation in nine districts of Madras State. The commercial production of hybrid seeds is rendered feasible due to the protogynous nature of the *cumbu* inflorscence and high natural cross pollination of 76 to 78 per cent that could be secured by planting the desired parents in alternate rows or as mixtures. (Rao, Nambiar and Krishnamurthi, 1949).

In the breeding of Sugar beet (*Beta vulgaris*, L.) crop in Sweden, heterosis is reported to be utilised. (Ramiah 1941). In America, the grain and forage yields of sorghum (*Sorghum spp.* Pers.) have been observed to be increased in many F1 hybrids, but the commercial production of hybrid Sorghums awaits the development of methods for economical seed productlon. (Bartel, 1949). The value of heterosis in increasing the yields of (*Solanum melongena*, L.) has been recognised both in Japan (Kakizaki, 1931) and India (Venkataramani 1946, Pal and Singh 1946). In cotton, the utility of heterotic inter-specific crosses has been realised by workers at Coimbatore (Ramanatha Iyer, 1936; Balasubrahmanyan and Narayanan, 1948) and Surat (Patel and Patel 1950). In every other crop, the phenomenon has been noted to occur in one cross or another and is increasingly tried to be exploited for economic ends. And it has been well realised that through its careful utilisation the breeder can make a substantial contribution to the World's food and possibly the World's clothes also.

Heterosis in Cotton: The cultivated cottons of the World belong to one or other of four different species of the genus *Gossypium L.* and fall under two distinct cytological groups. The American species, G. *hirsutum* and G. *barbadense* have 52 somatic chromosomes while the Asiatic species G. *arboreum* and G. *herbacum* possess 26 chromosomes. The two groups inter-cross freely, *only* among themselves and give rise to fertile hybrids frequently exhibiting pronounced heterosis in growth, yield and quality attributes. The Asiatic X American crosses seldom succeed and rarely give rise to sterile triploid hybrids. The intra and inter specific crosses within each of the two cytological groups alone offer scope for the economic utilisation of heterosis in cotton improvement.

All the four cultivated species of *Gossypium* have now come to engage the attention of breeders in many cotton growing countries of the World, and notably in the Madras State. The commercial crop of Madras comprises of ten different trade varieties falling under three botanical species viz. G. *hirsutum*, G. *arboreum* and G. *herbaceum*.

Since 1948 attempts are also being made to establish Sea Island cotton belonging to G. *barbadense* as a commercial crop in the coastal districts of Malabar and South Kanara and the initial results have been quite encouraging. During the past two decades, plant breeding work on cotton has generally been switched on to intensive hybridisation and exploitation of the variability thus created. While it may be stated that the chances of success through pure-line selection have almost been exhausted, the potentialities of hybridisation have also been fairly comprehended in recent times. Hence, at this stage, it may be pertinent to examine the possibilities of harnessing this biological phenomenon, viz. heterosis, for increasing cotton production and improving the quality of lint.

The frequent occurrence of heterotic crosses particularly in the interspecific group has been observed at Coimbatore and elsewhere, as recorded by many breeders. Very few workers have however attempted a specific study of the problem, Hutchinson, Gadkari and Ansari (1938) indicated the need for a proper understanding of heterosis in cotton for exploiting interspecific crosses in breeding work. More recently, Ramanatha Iyer (1946) pointed to the utility of hybrid vigour for augmenting yields in cotton and stressed upon the importance of determining the right type of combinations of crosses for raising yields to the maximum extent.

Since 1947, comprehensive studies on heterosis in cotton were undertaken at Coimbatore, using homozygous varieties drawn from all the four cultivated species of *Gossypium*. The results of investigations have brought out the great scope that exists for the practical utilisation of certain interspecific crosses in both the American and Asiatic groups of cottons. The data obtained from two such crosses between G. *arboreum* and G. *herbaceum* varieties as also one cross between G. *hirsutum* and G. *barbadense* are presented in this paper.

Material and Methods: The following parent types figure in the crosses.

I. Asiatic Species (n = 13)

1. Karunganni 5 (G. *arboreum*). A selection from interracial hybrid (*indicum* x *cernuum*) isolated at Coimbatore. It is a medium staple, quality cotton, released for general cultivation in the Karunganni tract by the Madras Agricultural Department.

2. Surat 1027 ALF. (G. *herbaceum*). A selection from Kumpta x Goghari hybrid, grown extensively in South Guzerat. It is one of the superior quality, *desi* strains of India.

3. *K F T 12–2–5* (G. *herbaceum*). A selection from Kumpta cotton of Bombay Karnatak. A medium staple, low ginning *desi* cotton, possessing cent per cent resistance to cotton wilt.

II. American Species (n=26)

1. *Cambodia 2* (G. *hirsutum*). A selection from Cambodia bulk, evolved at Coimbatore. A vigorous, prolific, medium staple cotton, widely cultivated in the Cambodia tract of Madras.

2. *Tanguis.* (G. *barbadense*). The commercial variety of Peru, South America. Very late in habit and a potential perennial cotton for South India. Noted for its coarse and strong lint.

The yield and quality attributes of the parent types are furnished in Table I.

Three crosses viz., Karunganni 5 x KFT 12-2-5, 1027 ALF x Karunganni 5 and Cambodia 2 x Tanguis were studied. The F1 hybrids along with the respective parent types were raised in randomised blocks adopting the replicated progeny row design of Hutchinson and Panse (1937).

The two Asiatic crosses and three parents were raised in unirrigated plots in the blacksoil block, while the American cross and parents were raised under irrigation in a red soil field. The agronomic treatments were the same as those given to Karunganni and Cambodia cottons respectively.

Observations on plant growth were made at fortnightly intervals by recording their height in centimetres and number of nodes produced. The plots were harvested plant-war and the yields recorded. The produce was examined for combed halo length in millimetres and ginning per cent (ratio of lint to seed cotton expressed as %).

The lint index (quantity of lint obtained from *Kapas* sample containing 100 seeds) and seed index (weight of 100 seeds) were also determined for each plant. As ginning per cent is largely influenced by seed weight, lint index which gives an exact measure of lint production without the bias of seed weight, was used for the estimation of heterosis in lint quantity.

The lint samples were bulked and examined for mean fibre length, and fibre weight per unit length. Their spinning performance was estimated by applying the formula evolved at the Technological Laboratory, Bombay. (Navkal and Sen, 1949).

The results were tested for significance by the analysis of variance. The manifestation of increased height, yield, lint length etc., in the first generation hybrid, as compared to the higher of the two parental values has been recognised as heterosis in interpreting the results.

Experimental Results: The results of observations are summarised in Table 1. The growth curves (height) of the two Asiatic hybrids exhibiting heterosis in plant height are shown n Figure 1.

I. *Asiatic Crosses:*

1. *Karunganni 5 x KFT 12-2-5.*

(G. *arboreum* x G. *herbaceum*).

The F1 hybrid has recorded significant heterosis in plant growth measured as height, yield of seed cotton and lint length. The increase in yield has been phenomenal, being 158% over the local parent viz. Karunganni 5 whose normal yields in the tract may be placed at 325 lbs. seed cotton per acre which has been realised in this experiment also. In lint production as recognised in lint indices, the hybrid is intermediate. The increase in *kapas* yield, more than compensates for the reduction in ginning per cent brought about through heterotic increase in seed weight of the F1. It is interesting to note that this hybrid has been estimated to spin 4 counts higher than either of the parents entering into the cross, due to its increased average fibre length.

2. *1027 ALF X Karunganni 5 (G.herbaceum x arboreum):* This hybrid is also significantly taller than either parent and has yielded 151% over the higher parent viz. Karunganni 5. The ginning percent of the hybrid is lower due to increased seed weight, but the lint yield is significantly higher than either parent due to appreciable increase in the yield of seed cotton. In spinning value it is better than Karunganni 5, but does not exceed the 1027 ALF parent which is a finer cotton possessing low fibre weight.

II. **American Crops:** 1. *Cambodia 2 XTanguis (G. hirsutum X G. barbedense):* In vigour of growth, as measured by plant height, the hybrid does not exhibit heterosis, but compares favourably with the local parent– Co. 2. Significant heterosis in yield of seed cotton and lint length are observed. The lint index of the hybrid is numerically higher than either parent and increased seed weight again exerts a bias towards lower ginning percent. The lint yields are however significantly higher than Co. 2. The improvements in quality are something quite remarkable, The hybrid has recorded higher average fibre length and lower fibre weight than either parent. As the lint is both longer and finer the spinning value has been appreciated to 52's as against 38's — 39's of the parents.

Discussion: All the parent strains utilised in these crosses represent improved, homozygous lines isolated as a result of selection within the respective species. The genetic differentiation of the species in *Gossypium* is consequent on the manifold gene substitutions during isolation (Harland 1936; Silow 1944; Hutchinson and Silow 1947) and subsequent accumulation of modifier complexes due to pressure of natural and artificial selection. It follows, therefore that in interspecific crosses divergent genetic systems are brought together in the F1 generation. There are accumulating evidences to show (Knight 1948) that several economic characters in cotton are controlled at least in part, by major genes, which in their dominant condition are favourable to growth and productivity. It is therefore suggested that the combination in the F1 of dominant favourable genes account for heterosis in quantitative characters like plant growth, yield of seed cotton. lint length and seed weight, observed in these interspecific crosses. The quality of lint has also appreciated due to heterosis in mean fibre length. It has been stressed (Nanjundayya, 1947) that 84% of the variation in spinning value could be accounted for when it was correlated with average length of fibre, and weight per inch. The Fl hybrids in the two Asiatic crosses have recorded slightly increased fibre weight per unit length than either of the parents. The increase in mean fibre length has however compensated for this 'coarseness' and kept the spinning value of the Fl's at appreciable levels. In the case of the American cross the mean fibre weight the Fl is lower than either parent. Such a feature was encountered by Balasubrahmanyan and Narayanan (1948) also in a cross between 4463 (*hirsutum*) X Maarad (*barbadense*). It is interesting to find that in this character the dominance bias in the two different groups of cotton is in the opposite direction. Further studies are under way to examine this question in detail.

It is suggested that these interspecific hybrids which have recorded phenomenal yield increases over the local improved strains, and possess appreciable quality attributes also, offer good scope for their large-scale extension towards the practical utilisation of heterosis for increasing the production of quality cottons in Madras State.

It has been realised that in a predominantly self-fertilised crop like cotton, the snag in the proposition lies in a cheap method for the production of hybrid seeds on a mass scale and the organisation needed for the same. Propagation of Fl hybrids by grafting (Vysotkii, 1932), mass production of crossed seeds by hand pollination (Ramanatha Iyer, 1936), and vegetative propagation of hybrid stem cuttings (Balasubrahmanyan and Narayanan (1948) are among the methods considered suitable for the large-scale cultivation of heterotic hybrids in cotton. Ramanatha Iyer (1936) who suggested the device of smearing the staminal column with clay paste for mass emasculation, estimated the additional cost of production of such hand-crossed seeds required for sowing an acre as Rs. 5/- and found that the yield increase of 40% obtained in his *arboreum* x *herbaceum* Fl hybrids left a residuum of extra profit of Rs. 7/- per acre, which was however not very attractive.

With the phenomenal increases of 100 to 150% in yield at appreciable levels of quality improvement, that have been obtained in the three interspecific crosses reported in this paper and with the attractive price levels for raw cotton obtaining now (approximately Rs. 1—6—0 per pound of 1″ staple cotton) it will be an economically sound proposition to produce and distribute hand-crossed seeds on a mass scale and intensify production of quality cotton at least as a short-term measure, in concentrated pockets around State farms, which can maintain crossing plots similar to nucleus areas for producing selfed seed.

Due to the perennial habit of the Tanguis parent the Cambodia 2 X Tanguis Fl hybrids can also be kept on the ground for two or three seasons as a perennial in vacant spaces and along bunds in water courses and the seed supply needs to be renewed in alternate years. Any extra pound of long staple cotton in these days of acute shortage of this important fibre crop should prove a valuable contribution to the Nation's wealth.

TABLE—I.

Heterosis in interspecific crosses in cotton

	Plant Growth		Productivity							Lint quality		
	Height in cms.	Nodes	Kapas yield gms./plant	Percentage on local parent (kapas yield)	Ginning percent	Lint yield gms./plant	Halo-length m.ms.	Lint index gms.	Seed index gms.	Average fibre longtgh inches	Mean fibre wt. x 10^{-6} oz. per inch	Calculated spinning value
I. Asiatic parents and hybrids.												
1027 ALF	53·0	30·5	5·63	83	29·5	1·26	24·1	2·86	6·75	0·86	0·155	35's
1027 ALF x Karunganni 5 F1	**77·4**	34·5	**16·91**	251	28·2	**3·66**	**26·8**	2·84	7·37	0·95	0·194	32's
Karunganni 5	60·2	35·5	6·75	100	30·4	1·73	25·2	2·63	6·03	0·88	0·189	25's
Karunganni 5 x KFT 12—2—5	**75·2**	36·3	**17·41**	258	25·7	**3·34**	**26·7**	2·25	6·47	0·95	0·204	29's
KFT 12-2-5	60·7	20·0	7·65	113	24·3	1·51	23·5	1·81	5·57	0·85	0·171	25's
Significance	Yes	No	Yes	...	Yes	Yes	Yes	Yes	Yes			
Critical difference	9·6	...	4·66	...	1·02	0·44	1·04	0·33	0·79		Bulk Samples	
II. American parents and hybrid.												
Cambodia 2	67·3	30·5	8·4	100	34·5	2·90	25·3	5·33	9·88	0·92	0·150	39's
Cambodia 2 x Tanguis F1	63·8	29·8	**16·5**	196	33·8	**5·58**	**30·8**	5·81	**11·37**	1·09	0·121	52's
Tanguis	47·4	38·7	3·0	36	34·0	1·02	25·8	4·53	8·83	0·92	0·176	38's
Significance	Yes	Yes	Yes	...	No	Yes	Yes	Yes	Yes		Bulk Samples	
Critical Difference	11·9	2·8	4·7	...	...	1·60	1·6	0·78	0·82			

N.B.— Bold figures denote significant heterosis.

SUMMARY

1. The beneficial effects of heterosis in agricultural characteristics of crop plants have inspired the economic utilisation of the phenomenon for the improvement of crops.

2. The theoretical concepts underlying heterosis and the role of the phenomenon in the breeding of maize, tobacco, tomato and *cumbu* are reviewed briefly.

3. Interspecific crosses in cotton are known to exhibit pronounced heterosis in yield and quality attributes. Their utility in cotton improvement is considered with reference to three hybrid combinations viz. Karunganni 5 X KFT 12–2–5 (G. *arboreum* x G. *herbaceum*) and 1927 ALF X Karunganni 5 (G. *herbaceum* x G. *arboreum*) in the Asiatic group and Cambodia 2 X Tanguis; (G. *hirsutum* x G. *Barbadense*) in the American group.

4. The two Asiatic hybrids have proved to be vigorous in growth and have recorded increases of 151% and 158% over the local parent Karunganni 5, in yield of *kapas* (seed cotton) at appreciable levels of lint quality. The American cross has recorded 96% yield increase over Cambodia 2 and the lint possesses superior fibre properties as well. By virtue of the late habit introduced from the Tanguis parent, this hybrid is fit for retention as a perennial for 2 to 3 seasons.

5. It is suggested that these heterotic hybrids, offer good scope for large-scale cultivation, at least as a short-term measure for intensifying the production of quality cottons in this State.

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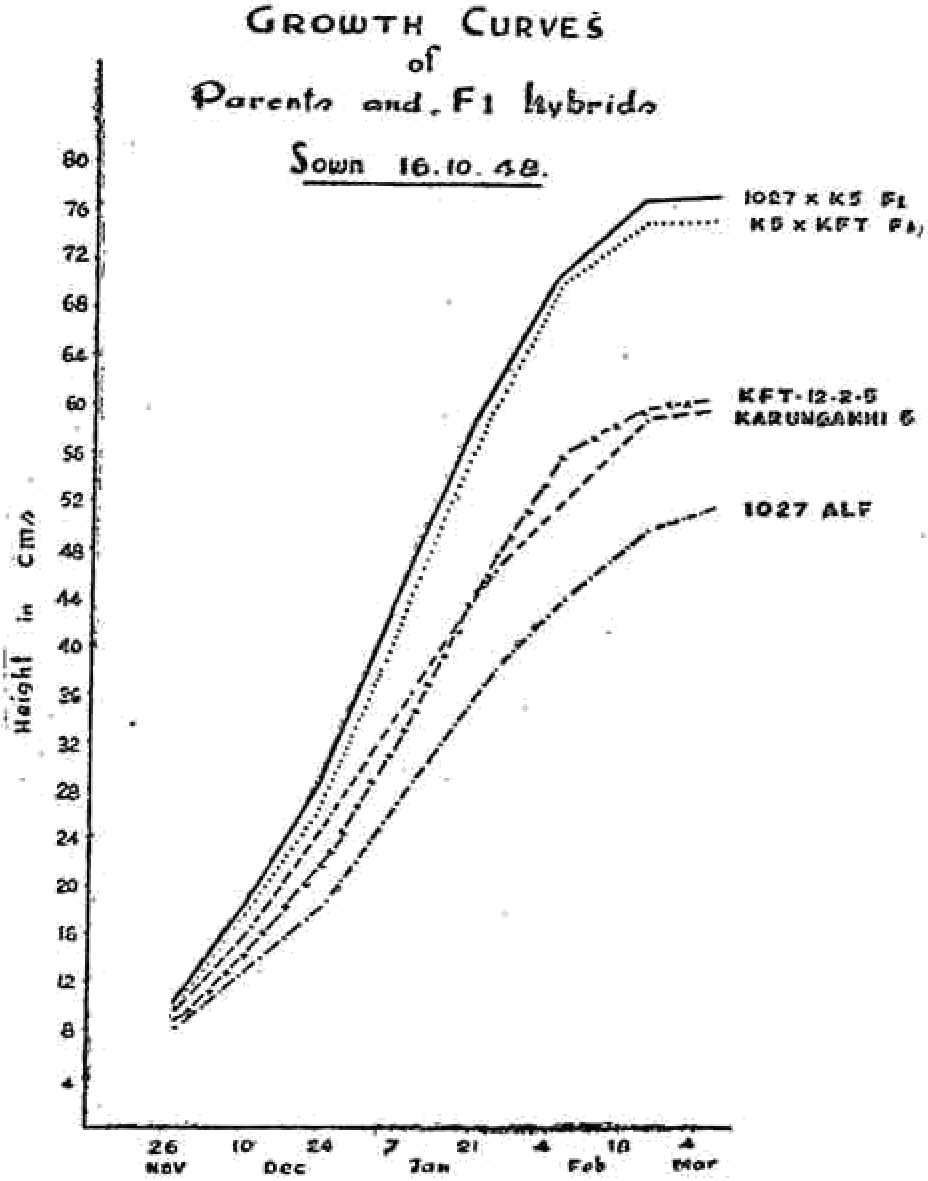
GROWTH CURVES
of
Parents and F1 hybrids
Sown 16.10.48.
Height in Cms
80
76
72
68
64
60
56
52
48
44
40
36
32
28
24
20
16
12
8
4
26 Nov
10 Dec
24
7 Jan
21
4 Feb
18
4 Mar
1027 x K5 F1
K5 x KFT F1
KFT-12-2-5
KARUNGAKHI 6
1027 ALF