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Putative genome donors of *Arachis hypogaea* (*Fabaceae*), evidence from crosses with synthetic amphidiploids

A. K. SINGH

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Abstract: Chromosome pairing, pollen and pod fertility in hybrids between cultivated tetraploid *Arachis hypogaea* and 15 synthetic amphidiploids from 8 diploid species (7 of the A genome and 1 of the B genome) of sect. *Arachis* have been utilized for the identification of putative genome donors in the evolution of cultivated *A. hypogaea.* These results, in conjunction with evidence from morphological similarities, phytogeographical distribution and some phytochemical features, confirm the segmental amphidiploid origin of *A. hypogaea. A. batizocoi* and *A. duranensis* are suggested as the donors of the B genome and the A genome respectively.

The species of the genus *Arachis* have been grouped into 7 sections on the basis of morphological affinities and their cross-compatibilities (GREGORY & al. 1973). The cultivated tetraploid species, *A. hypogaea* L. ($2n=40$), and a wild tetraploid species, *A. monticola* KRAP. & GREG., and a number of other diploid wild species, ($2n=20$) constitute the sect. *Arachis*. The identification of two pairs of marker chromosomes (a pair of distinctly small chromosomes and a pair with secondary constriction and a satellite) in *A. hypogaea* by HUSTED (1933, 1936), and the discovery of these chromosomes among diploid wild species have led to the inference that the two genomes are distributed among the diploids, and they, together, constitute the tetraploid species of sect. *Arachis* (SMARTT 1964, STALKER & DALMACIO 1981, SINGH & MOSS 1982). This has been confirmed by studies on interspecific hybridization between these species by GIBBONS & TURLEY (1967), SMARTT & GREGORY (1967), STALKER & WYNNE (1979) and through a comprehensive genome analysis by SINGH & MOSS (1984). All these studies have shown that the A genome is common to the majority of the investigated diploid wild taxa, and that the B genome is present only in *A. batizocoi* KRAP. & GREG. The two genomes are homoeologous, and they have together evolved the cultivated tetraploid species, *A. hypogaea,* through amphidiploidization (SMARTT & al. 1978, SINGH & MOSS 1984). GREGORY & GREGORY (1976) postulated that *A. cardenasii* KRAP. & GREG. nom. nud. (a perennial species) and *A. duranensis* KRAP. & GREG. nom. nud. (an annual species) are probably the diploid ancestors of *A. hypogaea.* However, SMARTT & al. (1978) from the interspecific hybridization postulated that *A. car-*

denasii and *A. batizocoi* are the two probable ancestors of *A. hypogaea*. Nevertheless, they proposed that confirmation of their hypotheses required production of amphidiploids from the two diploid wild species in various combinations, crossing these with tetraploid cultigens, and investigating meiosis and fertility in the resultant tetraploid hybrids, as has been done for other crop species such as tobacco, cotton, and wheat (CLAUSEN 1928, HUTCHINSON 1959, LILIENFELD & KIHARA 1951). This paper evaluated these hypotheses based on the data on chromosome associations at metaphase I, and pollen and pod fertility in the hybrids between *A. hypogaea* and 15 amphidiploids involving 8 diploid species of sect. *Arachis* representing both A and B genomes.

Materials and methods

The identities and sources of the eight diploid wild species, and the 5 cultivars of *A. hypogaea* used in the present study have been described by SINGH & MOSS (1982, 1984). Amphidiploids were produced in 34 combinations involving seven A genome and one B genome species of sect. *Arachis*. Of these, 22 amphidiploids were crossed as male parents with at least one cultivar belonging to both subspecies of *A. hypogaea*. 15 of these hybrid combinations were analysed cytologically, six involving AABB amphidiploids, and 9 involving AAAA amphidiploids, as reported ealier (SINGH 1986 b). The methods used for hybridization, and for cytological and pollen fertility analyses have been described by SINGH & MOSS (1984). Chromosome associations were analysed statistically using one-way analysis of variance (COCHRAN & COX 1957).

Results and discussion

On the basis of karyomorphological affinities SINGH & MOSS (1982) divided the diploid wild species of sect. *Arachis* into two clusters. One is represented by the majority of diploid species, which characteristically contain 9 pairs of long chromosomes and one pair of small chromosomes. The other represented by the lone species *A. batizocoi* does not have the pair of small chromosomes but has a pair of chromosomes with characteristic secondary constriction and a large satellite. Later a comprehensive genome analysis by SINGH & MOSS (1984) showed that interspecific hybrids between diploid species of similar karyotype have nearly normal chromosome associations (10 II) and a high pollen and pod fertility, whereas those involving *A. batizocoi* have a high number of univalents and almost no pollen fertility and no pod (seed) fertility. These studies therefore, provide strong support to the earlier hypothesis that among the investigated diploid wild species of sect. *Arachis*, there are several species with a similar genome called A and a single speices, *A. batizocoi,* with a fairly different genome, the B, each with a base number of 10 (SMARTT & al. 1978, SINGH & al. 1980, STALKER & DALMACIO 1981). Similarly, karyomorphological affinities and chromosome associations of nearly 10 II and 10 I in a majority of pollen mother cells (PMCs) of straight triploid hybrids between tetraploid *A. hypogaea* and these diploid wild species, all of the sect. *Arachis* (SINGH & Moss 1984) also supported that the two genomes distributed among the presently known diploid accessions of sect. *Arachis,* are together present in the cultivated species *A. hypogaea*. This supports the hypothesis of SMARTT & al. (1978) that hybridization between the two putative parental diploid species of sect. *Arachis,* one with an A genome and the other with the B genome, followed by doubling of chromosomes, evolved the wild tetraploid *A. monticola,* and the cultivated species *A. hypogaea*.

Table 1. Chromosome associations at metaphase I in F_1 hybrids between *Arachis hypogaea* and synthetic amphidiploids of diploid species of sect. *Arachis*. [1] Cytology of F_2 plants; [2] crossed with *A. hypogaea* subsp. *hypogaea*; [3] crossed with *A. hypogaea* subsp. *fastigiata*; [4] pollen and pod fertility in F_4; [5] in 1 plant out of 3; *N. S.* not scored; range for more than one plant

Cross	No. of cells analysed	Chromosome associations I	II	III	IV	% pollen stainability & range	No. of pods produced & range
A. hypogaea × synthetic amphidiploid F_1							
Intercluster (AB)							
(*batizocoi* × *duranensis*)[2]	16	3.3 ±0.54	16.4 ±0.57	0.7 ±0.24	0.4 ±0.13	29–62	1–5 (12–36)[4]
(*batizocoi* × *chacoense*)[1, 3]	14	2.2 ±1.70	16.2 ±1.82	0.4 ±0.48	0.9 ±0.80	N.S.	1
Reciprocal[3]	25	8.5 ±0.44	13.4 ±0.36	1.2 ±0.20	0.3 ±0.11	42	3
(*batizocoi* × *correntina*)[2]	16	4.9 ±0.47	15.1 ±0.41	0.5 ±0.16	0.8 ±0.14	37	2–4
(*correntina* × *batizocoi*)[3]	14	5.1 ±0.57	14.4 ±1.03	0.2 ±0.1	1.4 ±0.4	40–57 (52–70)[4]	2–4 (1–57)[4]
(*villosa* × *batizocoi*)[2]	25	4.7 ±0.43	15.5 ±0.38	0.8 ±0.16	0.5 ±0.12	33–63 (65–87)[4]	3–19 (22–70)[4]
Intracluster (AA)							
(*duranensis* × spec. GKP 10038)[3]	20	9.5 ±0.42	10.8 ±0.56	1.1 ±0.23	1.4 ±0.27	43–64	3–5
(*duranensis* × spec. HLK 410)[2]	12	6.8 ±0.81	14.5 ±0.34	1.2 ±0.27	0.2 ±0.11	67	
(spec. HLK 410 × spec. GKP 10038)[3]	25	10.1 ±0.54	11.5 ±0.60	0.8 ±0.19	0.9 ±0.19	18–35	34[5]
(spec. HLK 410 × *chacoense*)[3]	15	11.3 ±0.61	11.0 ±0.54	1.2 ±0.34	0.9 ±0.22	37	0
(*correntina* × *chacoense*)[2]	15	5.1 ±0.60	15.0 ±0.44	1.0 ±0.19	0.5 ±0.13	N.S.	0
(*correntina* × *villosa*)[2]	12	11.1 ±1.00	11.3 ±0.66	0.4 ±0.19	1.3 ±0.33	51	1
(*villosa* × *duranensis*)[3]	3	10.0 ±0.00	13.0 ±1.15	0.0 ±0.00	1.0 ±0.58	57–63	2
(*villosa* × spec. HLK 410)[2]	14	7.9 ±1.02	12.6 ±0.51	1.6 ±0.31	0.7 ±0.16	17–55	0 (0–14)[4]
(*villosa* × spec. HLK 410)[3]	35	8.7 ±0.41	11.9 ±0.32	1.1 ±0.15	1.0 ±0.16	N.S.	0
A. hypogaea × synthetic amphidiploid F_2							
(*batizocoi* × *duranensis*)[2]	13	2.9 ±0.60	16.3 ±0.68	0.7 ±0.26	0.6 ±0.18	40–62	20

Our observations on chromosome associations at metaphase I of the 15 Fl hybrids between *A. hypogaea* and inter-(AB) as well as intracluster (AA) amphidiploids showed that the mean bivalent associations were significantly higher in *A. hypogaea* × AABB amphidiploids than those from *A. hypogaea* × AAAA amphidiploids (Table 1). The exception was a reciprocal cross, (*A. batizocoi* × *A. chacoense* KRAP. & GREG.)^2 × *A. hypogaea,* which may be due to differences in cytoplasm of the reciprocal hybrid.

Most of the hybrids between *A. hypogaea* and AAAA amphidiploids formed more univalents and only 11 to 13 mean bivalents except *A. hypogaea* × (*A. duranensis* × *A.* spec. HLK 410)^2 and *A. hypogaea* × [*A. correntina* (BURKART) KRAP & GREG. nom. nud. × *A. chacoense*]^2 resulting in poor or no pod (seed) fertility. Further the chromosome associations observed in these hybrids were comparable and closer to the associations that were observed in *A. hypogaea* × AAAA *Arachis* spp. autotetraploids (SINGH 1986 a). This further supports that the genomes of the seven diploid species with A genome are similar. The high bivalent associations in two exceptional combinations (Table 1) may be due to certain genetic factors supporting bivalent formation that require further investigations. Nevertheless, the possibility of hybridization between a perennial and an annual species, both with similar genomes (A), followed by doubling of the chromosomes to evolve *A. hypogaea* as suggested by GREGORY & GREGORY (1976) is less. However, the hybrids between an AAAA amphidiploid and the two subspecies of *A. hypogaea* showed identical chromosome associations, suggesting a similar genomic constitution for the two subspecies of *A. hypogaea* (Table 1) thereby confirming the earlier observations of GREGORY & al. (1980) and SINGH & MOSS (1984).

The higher bivalent associations, and subsequently normal segregation of chromosomes resulting in comparatively high percentage of fertile pollen grains and pods in the hybrids between *A. hypogaea* and AABB amphidiploids indicates similarity between the genomes of these synthetic AABB amphidiploids and *A. hypogaea.* Therefore the hypothesis of an amphidiploid origin of *A. hypogaea* involving two diploid species, one with A, and the other with B genomes is strengthened. However, the meiotic cycle in these hybrids is not completely normal with 20 regular bivalents. This is not unexpected as modern representatives of both the diploid ancestors and the resultant tetraploid, cultivated *A. hypogaea* have passed through a long evolutionary process which has diversified them from their respective original forms.

As regards the species that gave rise to the earliest form of *A. hypogaea,* the data in Table 1 indicate that among the different hybrid combinations, the *A. hypogaea* × (*A. batizocoi* × *A. duranensis*)^2 amphidiploid had relatively the most regular meiotic cycle (Fig. 1 a, b). Besides this, unlike other diploid species of sect. *Arachis, A. batizocoi* and *A. duranensis* are annuals, and have many identical morphological features, such as branching pattern [main axis n has reproductive branches, and the laterals n+1, (the axes developing from the leaf axils of main axis n), has sequential reproductive branches (each node has a flower bearing axis in the axils of leaves)], less number of n+1 laterals, and leaf morphology, despite their different genomic constitutions. They are also distributed in the same region of southern Bolivia (Fig. 2) (VALLS & al. 1985). By virtue of their sympatric distribution, they should have had a greater opportunity for hybridization with each other than any other diploid species of sect. *Arachis* in an A and B genomic

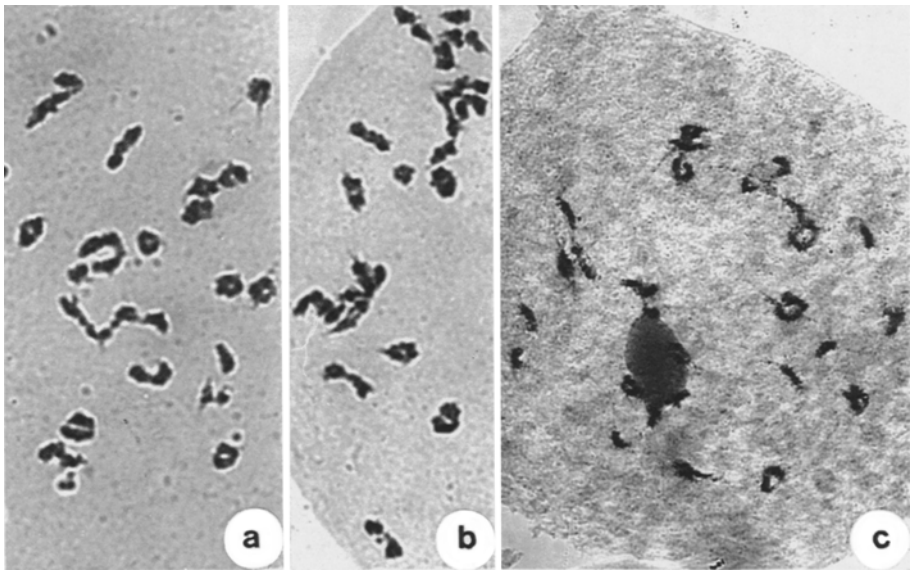

Fig. 1. Pollen mother cells in *Arachis* showing *a* 2 I + 14 II + 2 III + 1 IV; *b* 19 II + 2 I in *A. hypogaea* × (*A. batizocoi* × *A. duranensis*) amphidiploid; and *c* 17 II + 6 I in *A. hypogaea* × (*A. villosa* × *A. batizocoi*) amphidiploid

combination. The other diploid accession of this region, *A.* spec. GKP 10038, is a form of *A. duranensis* and is crossable as female only with *A. batizocoi* (Singh & Moss 1984). Krapovickas (1969, 1973) and Stalker (1985) also believed south of Bolivia and northwest Argentina, in the foothills of the Andes (Fig. 2) to be the most probable centre of origin of primitive *A. hypogaea* and *A. monticola.* The latter is considered a wild form of *A. hypogaea,* by Gregory & Gregory (1976) and Singh & Moss (1984). The primitive *A. hypogaea* subsp. *fastigiata* var. *fastigiata* (Valencia) (Stalker & Dalmacio 1986) also has morphological similarities with these two diploid species in having a sequential branching pattern, number of n + l branches, and leaf morphology. Therefore, it is logical to believe that hybridization between *A. batizocoi* and *A. duranensis,* followed by the doubling of chromosomes, may have led to an amphidiploid, which in turn evolved into *A. monticola* and *A. hypogaea* subsp. *fastigiata* var. *fastigiata.* Some phytochemical features, such as the flavonoid patterns of these diploid species, similar to *A. hypogaea* subsp. *fastigiata* (Krapovickas 1973) further support this contention.

But *A. hypogaea* contains two morphologically and genetically distinct subspecies, *A. hypogaea* subsp. *fastigiata* Waldlron and *A. hypogaea* subsp. *hypogaea* Krap. & Rig. Unlike *A. hypogaea* subsp. *fastigiata, A. hypogaea* subsp. *hypogaea* has the main axis (n) with only vegetative branches, and laterals (n + l) with pairs of vegetative branches (bearing normal green leaves) alternating with pairs of reproductive branches (Gregory & al. 1973). *A. monticola,* the wild tetraploid relative of *A. hypogaea,* also has two such forms (Gibbons 1966). Therefore, the next logical question concerns the origin of *A. hypogaea* subsp. *hypogaea.* There are two possibilities: it may have evolved through a mutation from *A. hypogaea* subsp. *fastigiata* that produced occasional vegetative branches in an otherwise sequential branching pattern or it may have evolved from a different species com-

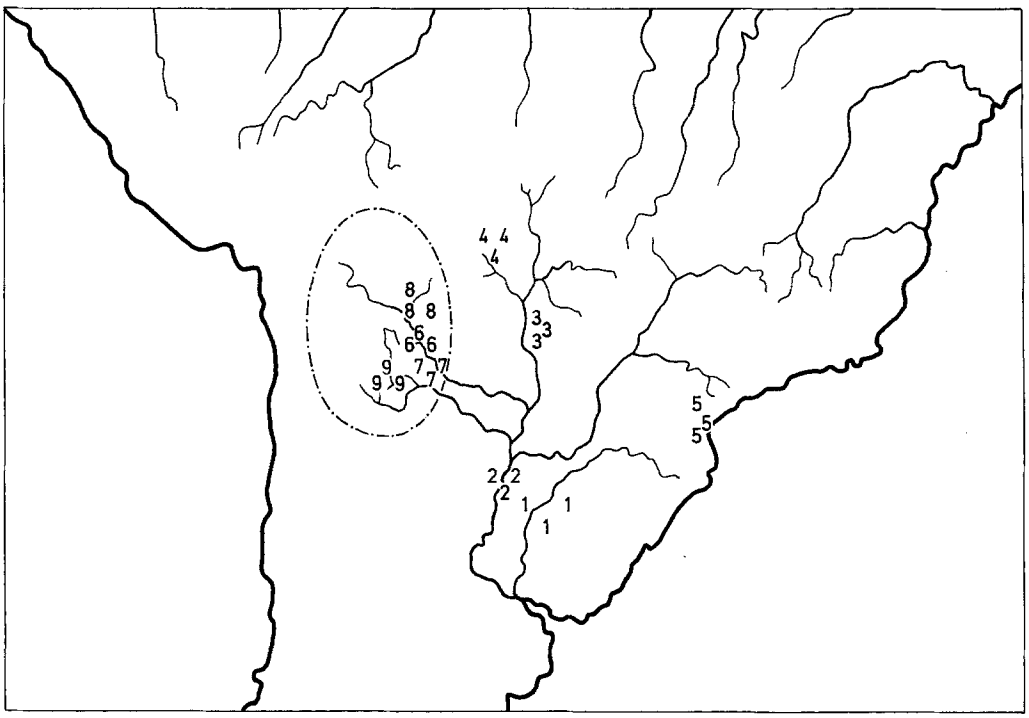

Fig. 2. Distribution of section *Arachis* species, in South America, with locations of known collections (up to 1982): *1 A. villosa, 2 A. correntina, 3 A. chacoense, 4 A. cardenasii, 5 A.* species HLK-410, *6 A. duranensis, 7 A.* species GKP 10038, *8 A. batizocoi, 9 A. monticola.* —·—·— Primary centre of origin for *A. hypogaea*

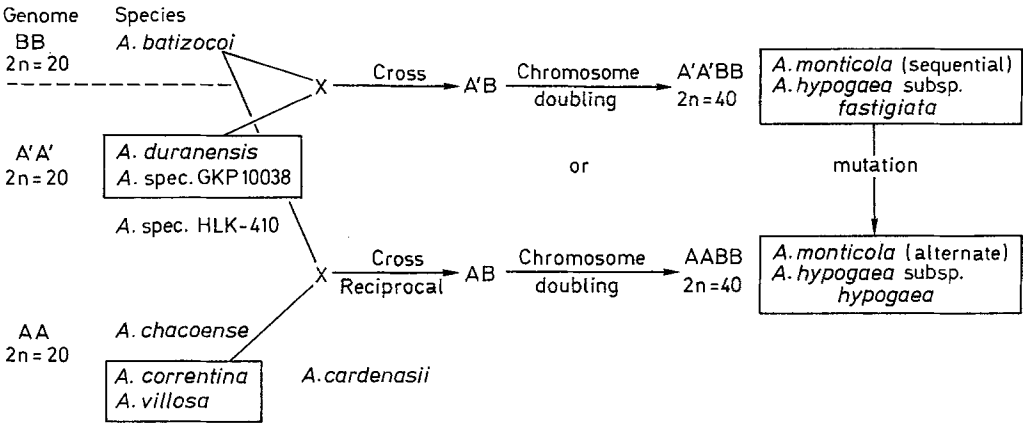

Fig. 3. Probable evolution of two subspecies of *Arachis hypogaea*. Species have been arranged to indicate relative affinities based on phytogeographical, morphological, phytochemical and cytogenetical evidence

bination of B and A genomes as proposed by SINGH & MOSS (1984) (Fig. 3). SINGH & MOSS (1984) considered the B genome of *A. batizocoi* a pivotal one like that of the A genome in tetraploid wheat (MAC KEY 1975). The B genome is common to both the subspecies of *A. hypogaea*, but either of these two subspecies involves

different cytoplasm or two different, but closely related, A genome species. The probability of a biphyletic origin is higher, considering the close phylogenetic relationships between A genome species, and their wide geographical distribution. They produce fertile hybrids with nearly normal meiotic cycle, despite the differences in their morphology and geographic distribution (STALKER & WYNNE 1979, SINGH & MOSS 1984).

For an independent origin of *A. hypogaea* subsp. *hypogaea* with a common *A. batizocoi* B genome, the most probable candidate contributing the A genome could be a perennial species with an alternate branching pattern. This should also have geographical and phylogenetic proximity both to diploid *A. batizocoi* and *A. hypogaea* subsp. *hypogaea. A. villosa* BENTH, *A. correntina* KRAP. & GREG. nom. nud. (*A. villosa* var. *correntina* BURKART) and other species such as *A. cardenasii* and *A. chacoense* could be the strong contenders. SMARTT & al. (1978) considered *A. cardenasii* to be the most probable taxon, but production of amphidiploids from hybrids between *A. batizocoi* and *A. cardenasii* in our studies do not give credence to such a hypothesis and also KLOZOVA & al. (1983) found this species distant from *A. hypogaea* on the basis of immunological affinities. *A. chacoense* is crossable only as a male parent with *A. batizocoi.* Therefore, among the perennial species, *A. villosa* and *A. correntina,* having no barriers to hybridization with *A. batizocoi* and to polyploidization, and showing similarities with *A. hypogaea* subsp. *hypogaea* and *A. monticola* in morphological features such as runner habit, prolonged growth period, similar branching pattern, absence of a compound spike inflorescence (KRAPOVICKAS 1969), and in their seed protein and enzyme profiles (CHERRY 1976), appear to be the most probable A genome donors to *A. hypogaea* subsp. *hypogaea.* High bivalent associations and pollen and pod fertility in the hybrids between *A. hypogaea* and the amphidiploids involving *A. batizocoi* with these two species (Fig. 1 c, Table 1) also indicate that each of these two species can be the probable donor of the A genome. An objection to this hypothesis may be that presently these two diploid species are distantly distributed from the main centre of diversity of *A. batizocoi* and *A. hypogaea* subsp. *hypogaea* (Fig. 2). However, further exploration in south of Bolivia, Paraguay and North of Argentina may change this situation. Nevertheless, the adaptation of a population to an ecological niche may also bring about such distribution changes and a population may become dominant away from its primary centre of origin. This is plausible as per the views of GREGORY & al. (1980) on the distribution of sect. *Arachis* spp. Sect. *Arachis* occurs mainly west of the 57° circle at the base of the last erosion surface exposed in the Pantanal along Paraguay across north central Bolivia to the skirts of the Andes where it was caught up in the Pleistocene uplifts, and where distinct new species mark the drainage systems (GREGORY & al. 1980).

Conclusions

The cytogenetic data suggest an amphidiploid origin of *A. hypogaea* and together with evidence from geographical distribution, morphological affinities and phytochemical factors suggest that its most probable ancestors are *A. batizocoi* and *A. duranensis.* The two subspecies of *A. hypogaea* and the two forms of *A. monticola* may have biphyletic origins. *A. hypogaea* subsp. *fastigiata* evolved from diploid species such as *A. batizocoi* and *A. duranensis* while *A. hypogaea* subsp. *hypogaea* probably evolved from diploid species such as *A. batizocoi* and *A. villosa.*

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Address of the author: A. K. SINGH, Groundnut Improvement Program, ICRISAT Patancheru P.O. 502324, A. P., India.